A new genus of Temnospondyli from the Triassic of Western Australia*

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Abstract

Early Triassic vertebrates recently collected in Western Australia include two species of a new genus of Amphibia (order Temnospondyli) which is closely allied to *Rhytidosteus capensis* of the Cynognathus Zone of South Africa and to *Peltostega erici* and *P. wimani* of the Posidonomya beds of Spitzbergen. The type species, based on four partial skulls, a lower jaw and numerous skull, lower jaw, and dermal shoulder girdle fragments, occurs in exposures of the lower Triassic Blina Shale of the West Kimberley District. The second species is based on a partial skull found in a core sample of the Kockatea Shale from an exploratory oil well in the Southwestern District. A new superfamily (Rhytidosteoidea) and a revived family (Rhytidosteidae) are proposed to receive *Rhytidosteus*, *Peltostega* and the new genus *(Deltasaurus)*. The close relationship of the well core species of the type species supports microfloral evidence for the contemporaneity of the Kockatea and Blina Shales.

Introduction

The Blina Shale is exposed in three large synclines at the northwestern end of the Fitzroy trough in the West Kimberley District and narrow strips of outcrop have been mapped in the northeastern part of the Canning Basin more than 300 miles southeast of Derby. Exploration wells in the large syncline which extends inland from the coast at King Sound disclose thicknesses from 650 feet to 1,000 feet. The shale forms clay soil plains with occasional residual rubbles. Outcrops are rare and no type section has been designated. The upper 100 feet, consisting of thinly bedded sediments, are exposed in steep slopes on the southern flank of the Erskine Range near the Great North Highway, 70 miles southeast of Derby. These slopes contain the principal localities at which fossil vertebrate material has been collected.

The first collection of vertebrate fossils from the Blina Shale was made in 1953 by field parties of the Bureau of Mineral Resources during an investigation of the geology of the Fitzroy Trough. Brunnschweiler (1954, p. 42-44) recognized the Triassic age of the vertebrate and invertebrate fossils and redefined the unit as a Formation to be included with the overlying Erskine Formation in the Derby Group. His report is supplemented with further description and mapping by the Bureau of Mineral Resources (Guppy and others, 1958 and Veevers and Wells, 1961) and a summation is given by McWhae and others (1958, p. 82-83). Vertebrate material in the collection of the Bureau of Mineral Resources was lent to the University of California Museum of Paleontology for study by the author.

A more extensive collection was made in June and July, 1960 by a joint expedition of the Western Australian Museum and the University of California Museum of Paleontology. Personnel included Dr. C. L. Camp of the Department of Paleontology, University of California as party leader, Dr. W. D. L. Ride, Director of the Western Australian Museum, Dr. K. G. McKenzie, then of the University of Western Australia, Mr. D. Merrilees of the Western Australian Museum and the author. Camp (1963) has contributed a history of the expedition which describes field activities in the Fitzroy trough and also an unsuccessful search for fossil vertebrates in the Northern Territory. McKenzie (1961) mapped the fossiliferous localities and investigated the stratigraphy. His report includes a synopsis of the field work, detailed descriptions of the lithology and vertebrate localities, a locality map and an analysis of the depositional environment.

The specimens obtained by the expedition are divided between the two institutions according to agreement. In addition to the genotypic species described in this report the Blina fauna includes four other temnospondylous amphibians, a coelacanth, a lungfish, an actinopterygian, shark teeth, large pieces of bone which may represent a marine reptile and enigmatic platy structures of organic origin which may be derived from a vertebrate. Subsequent papers will include descriptions of these latter forms and analyses of the paleoecology and stratigraphic significance of the Blina vertebrate fauna.

The Blina Shale also contains plant and invertebrate fossils. Balme (1963) has identified the microplankton and microflora. He also notes the presence of " . . . equisetalean, and probably lycopodiaceous, stem fragments." at

the Erskine Range exposures. *Isaura* and *Lingula* from Fitzroy Trough are noted by Brunnschweiler (1954) and McKenzie (1961). Invertebrate fossils from Blina exposures in the northeastern Canning Basin (Veevers and Wells, 1961, p. 110) include *Isaura, Lingula* and a pelecypod, cf. *Pseudomonotis*, (all determined by R. O. Brunnschweiler), and a worm burrow, *Diplocraterion*, (determined by A. A. Öpik). An internal cast of a cephalopod shell, too poorly preserved for identification, was found on the surface at the Erskine Range.

A partial skull, referred to the genus founded for the Blina amphibian in this report, was found in a core sample of the Kockatea Shale of the Perth Basin. B.M.R. 10 (Beagle Ridge Bore) was drilled in 1959 on the western coast between Perth and Geraldton by Oil Drilling and Exploration (W.A.) under contract to the Bureau of Mineral Resources. The occurrence has been described by Dickins, McTavish and Balme (1961).

The formation has only one surface exposure of some 25 feet at Kockatea Gully near its junction with the Greenough River (Playford and Willmot, in McWhae and others, 1958, p. 83). Various bores in the basin record thicknesses from 1,091 feet to 1,531 feet. The surface exposure and core samples from the bores are siltstone, shales and sandstones.

The microflora and invertebrate fauna from B.M.R. 10 offer precise evidence for assigning an age to the Kockatea skull and, by inference, to the vertebrate fauna of the Blina Shale. Mesozoic vertebrates rarely occur in sediments which have been directly dated by plant and invertebrate fossils and the singular good fortune of finding a vertebrate fossil in a well core is augmented by this association. Balme (1963) has described the microplankton and microflora from B.M.R. 10, from Kockatea cores taken from other wells and from the surface exposure, noting the occurrence of many of the same taxa in the Blina Shale. He equates the Blina and Kockatea Shales in time, assigning an early Scythian age to both. The invertebrates from B.M.R. 10 (Dickins and McTavish, 1963) include "*Lingula*", five pelecypods, three ammonites and an annelid. The composite fauna is early Scythian. Two of the ammonites, *Ophiceras* cf. *subkyoticum* and *Subinyoites kashmiricus* more precisely limit the age of the sediments in the bore from 2,405 feet to 2,812 feet to the Otoceratan Zone, lowest division of the Scythian. The vertebrate skull was found near the centre of this section in core 28 (2,614-2,624 feet).

Occurence and preservation of the Blina vertebrate fossils

Vertebrate fossils are rare in the formation and are concentrated in a few productive localities. Most of the extensive exposures on the flanks of the Erskine Range are barren. Many small outcrops and rubble heaps in the Fitzroy Valley were prospected but failed to produce any material. Several localities contain only scattered and isolated pieces of bone. A few small pockets of bone were found in the quarries at the Erskine Range but no bone beds or extensive concentrations were discovered.

The condition of the vertebrate fossils suggests that they had been transported by water, but perhaps for no great distance. Most of the fossils are broken and some show worn surfaces which may have been caused by abrasion during transport. No articulated skeletal elements were found. Only the larger and more massive structures such as dipnoan teeth, ethmoidal bones of *Saurichthys* and skulls, lower jaws, dermal shoulder elements and atlases of amphibians occur as common fossils. It is probable that the skeletons were broken up and scattered either prior to or during transport and that the smaller and more delicate pieces of bone were macerated or otherwise destroyed. Perhaps some of the broken and scattered occurrence of the specimens and the scarcity of the smaller, more fragile bones is due to predator action but no tooth marks or other evidence of predation were found on any of the specimens.

Surface material from the localities consists principally of the internal cores and external impressions of amphibian skulls and lower jaws; the original bone has been completely eroded from most of those. The cores retain impressions of the inner surfaces of the dermal bones and also casts of the vacuities and foramina. It has been possible in many instances to reconstruct the original specimens from these casts and impressions with reasonable certainty.

The preservation of bone in specimens from the Erskine Range quarries is generally poor. The bone is splintery, porous and extremely friable. The permineralizing substance, obviously rich in iron compounds, is purple, dark red and brown. In many instances the bone was both too poorly preserved and too delicate to save. In such cases the bone was carefully removed from the internal and external impressions of the specimens and latex peels were taken from these impressions. Preparation of quarry specimens was further complicated by the frequent presence of hard lumps of hematite that adhered to the surfaces.

Fossil vertebrate localities in the Blina Formation

The University of California Museum of Paleontology locality designation and Bureau of Mineral Resources locality designations in the following text are substituted for the locality designations used by McKenzie 1961 as follows:

U.C.M.P. locality V 6040 = McKenzie, fig. 1, p.70, locality 4 (quarries 1, 2 and 3);

U.C.M.P. locality V 6042 = McKenzie, fig. 1, p.70, locality 7;

U.C.M.P. locality V 6043 = McKenzie, fig. 1, p.70, locality 8;

U.C.M.P. locality V 6044 = McKenzie, TABLE II, p.73, ninth entry ("Bore 6, Noonkanbah Station. 124° 45' E., 18° 20' S.");

B.M.R. locality = McKenzie, TABLE 11, p.73, eighth entry ("Dry Corner area, Nerrima Station. 124° 05' 30" E., 18° 21' S.").

U.C.M.P. localities V 6040 and V 6042 are just south of the Great North Highway, 69 miles southeast of Derby, on the south slopes of the small butte which is an outlier of the Erskine

Range. Locality V 6043 is on the southern slope of the main body of the Range north of the highway. To reach locality V 6044, drive car 25 miles north from Noonkanbah Homestead on the station road leading to Calwynyardah Homestead; the locality is a low rounded hill 1½ miles ENE of Noonkanbah Bore no. 20. The B.M.R. locality produced the material noted by Brunnschweiler (1954). Unfortunately the original field notes were destroyed in a fire at the Bureau of Mineral Resources offices in Canberra and the exact location of the site was thereby lost. Dr. Ride corresponded with two members of the B.M.R. field party and in their recollection the locality was on a rise close to a gate on a road between Dry Corner Bore and Tutu Bore. Although the Dry Corner area was searched on two separate occasions by the W.A.M.-U.C.M.P. field party the locality could not be re-established. To reach the approximate area in which the fossils were found turn south from Luluigui Homestead and drive 4 miles to Moore's Bore and 8 more miles to Waterford's Bore. Turn east and drive 10 miles to Dry Corner Bore. The only fence gate on this latter section of road, 1 mile east of Dry Corner Bore, is astride a small sand dune. No other roads between Dry Corner Bore and Tutu Bore could be found. It is possible that the sand accumulation at the gate is recent and has thoroughly covered the site.

Abbreviations for all figures

a.p.v.	....	....	anterior palatal vacuity
Ang	....	....	Angular
c. bo	....	....	basioccipital space
c. so	....	....	supraoccipital space
ca. ct	....	....	chorda tympani canal
Co	....	....	Coronoid
d	....	....	denticle
d. t	....	....	dentary teeth
Den	....	....	Dentary
Ecpt	....	....	Ectopterygoid
Eo	....	....	Exoccipital
f	....	....	foramen
f.c.t.	....	....	chorda tympani foramen
f. m	....	....	foramen magnum
f.m.p.	....	....	posterior meckelian foramen
f. p	....	....	parietal foramen
fa. a	....	....	articular facet
fe. po	....	....	pteroccipital fenestra
fi. pq	....	....	palatoquadrate fissure
fo. ad	....	....	adductor fossa
fo. pt	....	....	posttemporal fossa
fo. st	....	....	subtemporal fossa
Fr	....	....	Frontal
Ico	....	....	Intercoronoid
ip. v	....	....	interpterygoid vacuity
Ju	....	....	Jugal
m. t	....	....	maxillary teeth
Mx	....	....	Maxillary
n. e	....	....	external naris
n. i	....	....	internal naris, choana
Na	....	....	Nasal
or	....	....	orbit
P	....	....	Parietal
p. c	....	....	cultriform process
p. h	....	....	hamate process
p. l	....	....	lamellosus process
p. po	....	....	paraoccipital process
p. poc	....	....	postcondylar process
p. prc	....	....	precondylar process
p. pt	....	....	ascending process of the pterygoid
p. quj	....	....	descending process of the quadratojugal
p. ra	....	....	retroarticular process
p. sq	....	....	descending process of the squamosal
p. st	....	....	subotic process
p. v	....	....	vertical process
Pa	....	....	Prearticular
Pco	....	....	Precoronoid
Pf	....	....	Postfrontal
Pl	....	....	Palatine
Pm	....	....	Premaxillary
Po	....	....	Postorbital
Pos	....	....	Postsplenial
Pp	....	....	Postparietal
Prf	....	....	Prefrontal
Ps	....	....	Parasphenoid
Pt	....	....	Pterygoid
Qu	....	....	Quadrate
Quj	....	....	Quadratajugal
r. pl	....	....	palatal ramus of the pterygoid
r. qu	....	....	quadrate ramus of the pterygoid
s. io	....	....	infraorbital groove
s. j	....	....	jugal groove
s. m	....	....	mandibular groove
s.o.	....	....	occipital groove
s. so	....	....	supraorbital groove
s. t	....	....	temporal groove
Sa	....	....	Surangular
Sp	....	....	Splenial
Sq	....	....	Squamosal
St	....	....	Supratemporal
sym	....	....	symphysial region of lower jaw or symphysial surface
sym. t	....	....	symphysial tusk
t	....	....	Tusk or tusk pit
Tab	....	....	Tabular
Vo	....	....	Vomer

Superfamily Rhytidosteoidea, n, superf.
Family Rhytidosteidae, von Huene, 1920, pp. 212 and 458

The family Rhytidosteidae, with *Rhytidosteus* as type genus, is revived and amended to include *Peltostega* and the new genus from Western Australia. The unity of this group was realized through comparison of the African and Spitzbergen genera with the new genus.

Peltostega and *Rhytidosteus* both have laterally placed orbits and broad cultriform processes of the parasphenoids. Further direct comparisons, however, were not possible as the only illustrated portions of *R. capensis* were the antorbital portion and the exoccipital, and the *Peltostega* specimens are all posterior skull portions.

The definitive characters of the Rhytidosteidae cited by von Huene (1920, p. 458) are: broad, triangular skull; orbit laterally placed; probably a short broad interpterygoid vacuity. Woodward (1932, p. 217), Kuhn (1933, p. 101) and Case (1946, p. 400), followed von Huene in placing *Rhytidosteus* in its own family. Romer (1947, p. 314; 1950, p. 590), and Kuhn (1960, p. 70) included *Rhytidosteus* in the Trematosauridae. Von Huene (1948, p. 69) revised his original classification and placed the genus in a new family, Lyrocephalidae with *Lyrocephalus* and *Peltostega*.

Romer (1945, p. 590; 1947, p. 314), Case (1946, p. 406), and Kuhn (1933, p. 75; 1960, p. 70), have included *Peltostega* in the Trematosauridae. Jaekel (1922, p. 5) regarded the genus as a Triassic survival of the Sclerocephalidae, a referral based on the short triangular skull and the central location of the orbit on the skull roof. The superficial appearance of Wiman's reconstruction led Woodward (1932, p. 216) to include Peltostega in the Metoposauridae.

Säve-Söderbergh (1935, pp. 87-88), erected a new family, Peltostegidae. The familial characters were: a broad triangular skull with a very

growth on the skull roof; the very lateral position of the orbit, situated close behind the sagittal midpoint of the skull; and the broad and dorsoventrally thin cultriform process which lacks a ventral longitudinal ridge.

Nilsson (1946, pp. 47-48) erected a new superfamily, Peltostegoideae, to emphasize the distinction of *Peltostega* from the Trematosauroideae. He greatly expanded the characterization of the Peltostegidae. Most of his characters are diagnostic only of the genus and are not germane to this discussion. Several of his observations on the occiput and posterior part of the palate, however, are also applicable to the new genus and may prove to be rhytidosteid characters if new genera of this family are found or if more material of *Rhytidosteus* is recovered: the posterior border of the interpterygoid vacuity is broad; the pteroccipital foramen is large and is visible in posterior view; the ascending process of the pterygoid is partly separated from the descending process of the squamosal by a palatoquadrate fissure.

The family characters of von Huene (1920), for the Rhytidosteidae and of Säve-Söderbergh (1935) for the Peltostegidae which have been quoted in the above discussion are incorporated into the definitions.

Features of the Blina genus which are shared by each of the other two genera are discussed in later passages of this report. These support the concept of the family but there is no certainty that any of them occur in all members of the family and they cannot be regarded as definitive.

It is quite likely that the Rhytidosteidae originated among the Rhinesuchoidea of the late Permian. The Capitosauridae also had their origins within this group. As the rhytidosteids are as fully distinct as the capitosauroids from this basal superfamily, consistency within the classification is best served by placing the family in a new superfamily.

Definition and diagnosis of the superfamily and family

Triassic temnospondyls with broad, triangular skulls and very wide occiputs. Orbits near centres of lateral margins, facing dorsolaterally. Cultriform processes of parasphenoids exceptionally broad. Sculpture of dermal bones dominated by radiating ridges which bear prominent nodes at points of junction and bifurcation. Otic notches and tabular horns triangular and proportionately small.

Quadrates on same hinge line as exoccipital condyles rather than posterior to them as in rhinesuchids, lydekkerinids and uranocentrodontids. Skulls lack: parabolic outlines, rudimentary otic notches, U-shaped palates and modifications of occipital processes of squamosals and pterygoids characteristic of brachyopids; elongate postorbital regions of skull roofs, high, narrow occiputs and extensive parasphenoid bones, underplating exoccipitals, of trematosaurids; posterior slope of occiputs, as viewed from above, and anterior positions of orbits of metoposaurids; posterior, closely spaced orbits of capitosaurids; peculiar construction of occiput and "closed" otic notch of *Laidleria;* Lamellosus crest present, absent in *Laidleria.*

Deltasaurus, gen. nov.

Type species. Deltasaurus kimberleyensis
Distribution. Blina Shale and Kockatea Shale, Western Australia.
Definition and diagnosis of the genus. Skull short and triangular. Orbit oval with an indented anterolateral margin.

Snout broader and more rounded, external nares closer to snout tip, dermal bone structure finer and more regular, radiating ridges of sculpture straighter, lower jaw shallower than in *Rhytidosteus.* Orbits over centers of interpterygoid vacuities, over anterior edges of interpterygoid vacuities in *Rhytidosteus.* Retroarticular process of lower jaw pointed, notched in *Rhytidosteus.*

Pits of sculpture on dermal bones of skull roof less pronounced, grooves of lateral line system more continous, parasphenoid-pterygoid suture relatively longer, quadrate ramus of pterygoid longer and narrower, (?) palatal shagreen better developed than in *Peltostega.* Exoccipital-pterygoid suture present, absent in *Peltostega.*

Deltasaurus kimberleyensis, sp. nov.
(figs. 1-9)

Holotype. W.A.M. no. 62.1.44, a partial skull roof with associated palate fragment.
Type locality. U.C.M.P. locality V 6040, Blina Formation, West Kimberley District, Western Australia.
Paratypes. Incomplete skulls, U.C.M.P. nos. 61063 and 61064, from U.C.M.P. locality V 6040; incomplete skull, U.C.M.P. no. 61062, from U.C.M.P. locality V 6042; skull fragments, U.C.M.P. nos. 61061, 61135, 61142, 61232, 61277, 61306, 61308, 61309, 61310, 61313, 61314, 61380, 61381, 61383, 61384, 61385, 61386, 61387, 61390 and 62156, all from U.C.M.P. locality V 6040; incomplete articulated lower jaws, U.C.M.P. no. 61098, from U.C.M.P. locality V 6043; lower jaw fragments, W.A.M. nos. 60.9.16 and 64.7.17 and U.C.M.P. nos. 61068, 61071, 61072, 61073, 61100, 61101, 61102, 61103, 61104, 61105, 61106, 61107, 61108, 61110, 61111, 61112, 61114, 61116, 61118, 61119, 61120, 61122, 61123 and 61126, all from U.C.M.P. locality V 6040; lower jaw fragments, U.C.M.P. nos. 61099, 61117, 61121, 61127, and 64972, all from U.C.M.P. locality V 6042; lower jaw fragment, U.C.M.P. no. 62158, from U.C.M.P. locality V 6044; lower jaw fragments, B.M.R. nos. F21794, F21805, F21807 and F21817 from B.M.R. locality; clavicles and clavicular fragments, U.C.M.P. nos. 61080, 61082, 61083, 61084, 61085, 61087, 61137 and 61307, all from U.C.M.P. locality V 6040; clavicular fragments, U.C.M.P. nos. 61092 and 61237, from U.C.M.P. locality V 6043; interclavicular fragments, U.C.M.P. nos. 61124, 61130, 61131, 61139, 61322, 61325, 61326 and 61327, all from U.C.M.P. locality V 6040; interclavicular fragment, U.C.M.P. no. 61319, from U.C.M.P. locality V 6043.
Diagnosis of the species. A *Deltasaurus* with punctate sculpture, dominated by straight, broad occiput; the lack of zones of intense

narrow ridges radiating out from bone centers. Posterior border of external naris straight. Width across posterior borders of orbits relatively greater than in Kockatea species.

Description

Skull roof (figs. 1a, 2d, 3a and 4a). The dimensions and most of the restoration of the skull roof (fig. 4a) are taken from the holotype, W.A.M. no. 62.1.44 (fig. 1a). This speci-men preserves the internarial region and most of the left side. The shape and position of the orbit and external naris, most of the borders of the individual bones and the character of the surface ornament are all clearly established by this specimen. U.C.M.P. no. 61064 (fig. 3a), the left posterolateral corner of a much smaller skull, has contributed the otic notch, several sutures and much of the occipital border.

Fig. 1.—*Deltasaurus kimberleyensis* gen. et sp. nov., holotype W.A.M. no. 62.1.44 (U.C.M.P. locality V 6040); skull: a, dorsal view; b, ventral view. x 0.58.

The holotype was found ventral side up and close to the surface at V 6040. It was completely encased in concretionary iron. It includes the anterior portion of the palate in addition to the incomplete skull roof. The actual bone of the specimen was too badly preserved and the enclosing matrix too hard to allow normal preparation. The concretionary iron of the palate fragment was ground away until the tiny tips of the denticles of the palate were exposed at a level of 1mm. above the palate. The palate portion was then carefully removed from the specimen. The powdery remnants of skull roof bone were cleaned from the external mold of the dorsal surface with the aid of a 10X microscope. A latex positive

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was then taken from this mold. Plaster molds of the latex were made and then plaster positives were taken from the plaster molds.

The distinctive skull shape, which approaches an equilateral triangle, has been restored from the angle between the median suture between the premaxillaries and nasals and the intact left lateral border of the holotype. The snout is bluntly rounded and the posterolateral corner is angular. U.C.M.P. no. 61064 shows an angular otic notch and tabular horn. The occipital border of this specimen is slightly convex anteriorly about the midline.

The position of the orbit is one of the most striking features of the skull roof. It is widely removed from the midline and lies close to the midpoint of the lateral margin. It faces outward and somewhat upward. It has rounded medial and posterior borders, a flattened lateral border and an angular anterior border. The
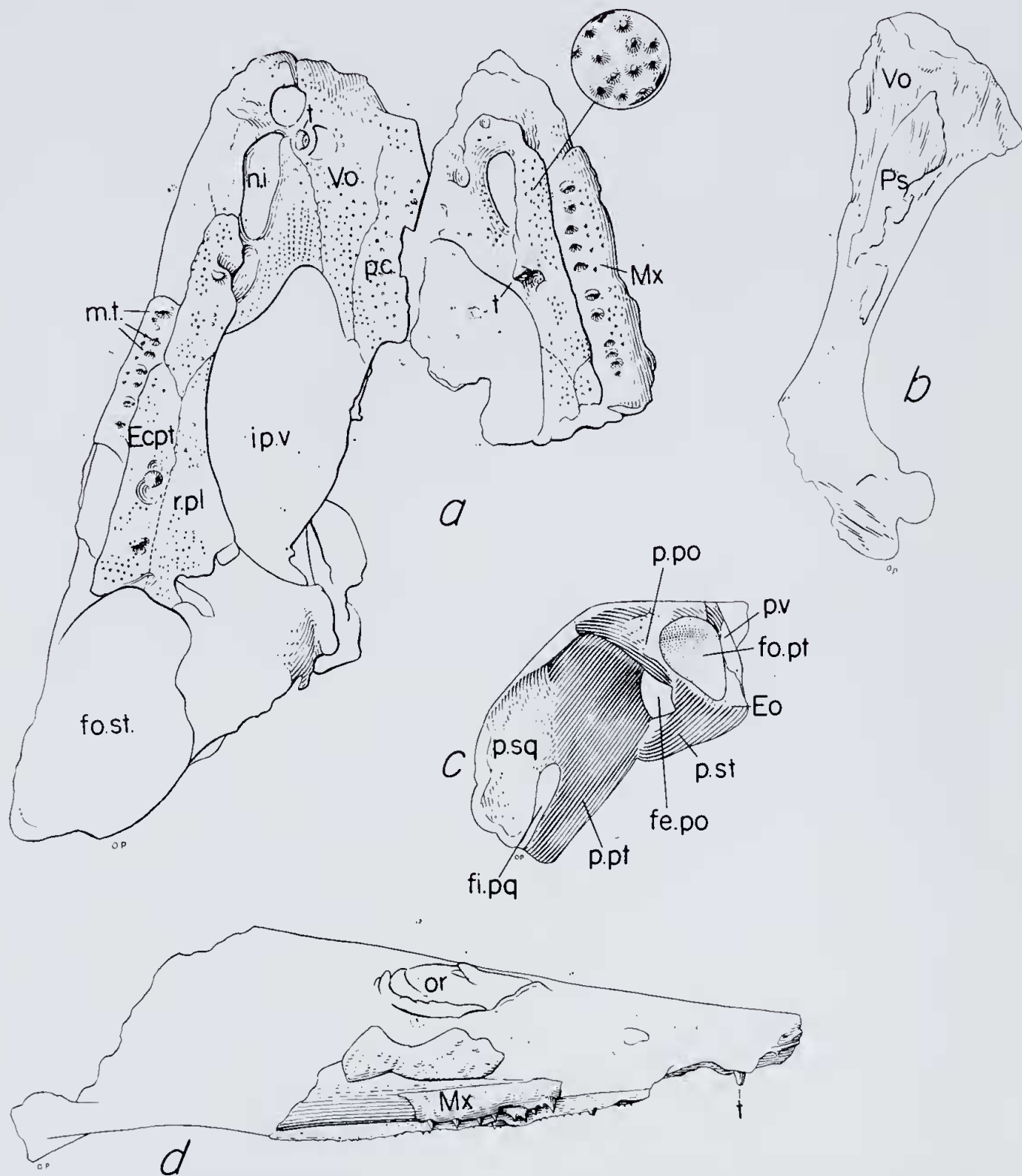
Fig. 2.—*Deltasaurus kimberleyensis* gen. et sp. nov., paratypes: a, U.C.M.P. no. 61063 (U.C.M.P. locality V 6040), skull, palatal surface; b, U.C.M.P. no 61061 (U.C.M.P. locality V 6040), palatal fragment, ventral view; c, U.C.M.P. no. 61062 (U.C.M.P. locality V 6042), skull fragment, occipital view; d, U.C.M.P. no. 61063 (U.C.M.P. locality V 6040), skull, lateral view. All x 0.63.

orbit is small relative to the skull area. The borders of the orbit are flush with the surrounding skull surface.

The external naris also lies far laterally. The naris is longer than broad, has rounded anterior and medial borders and a flattened lateral border.

The angular otic notch of U.C.M.P. no. 61064 is rather small and shallow compared with those of most other labyrinthodonts.

The dorsal surface of U.C.M.P. no. 61062 shows that the quadratojugal was produced posteriorly into a horn-like process.

The skull probably had a parietal foramen. Its position on the midline suture of the parietal bone is hypothetical.

The broad central area of the skull roof between the nares, orbits and otic notches is either flat or slightly convex. The lateral region between the naris and orbit curves sharply down from the flat skull table to the posterolateral corner of the skull.

There is no lacrimal bone, and the prefrontal and maxillary are in contact. Otherwise the bones of the skull roof have the standard labyrinthodont arrangement.

The paired median roofing bones are broad and occupy most of the broad skull table. The front of the premaxillary is missing; its anterior border is restored from the trend of the marginal tooth row of the palate fragment. The nasal and frontal, quite similar in shape, are broad and quadrangular. They have convex anterior and lateral borders and concave posterior borders. The posterolateral corner of the frontal indents the anterior margin of the parietal bone. The parietal is the largest bone of the skull roof. It has irregular anterior and lateral borders and a straight posterior border on the postparietal. The postparietal is only half the length of the parietal. It has an angular lateral border, anterolaterally bounded by the supratemporal and posterolaterally by the tabular.

The prefrontal, postfrontal, postorbital and supratemporal are roughly equivalent in area and are slightly curved in section. They are considerably smaller than the elements of the paramedian series. The prefrontal forms the anterior border of the orbit and, anteriorly, it projects between the maxillary and nasal; medially it is bordered by the nasal and frontal. The postfrontal forms most of the medial margin of the orbit; it projects between the prefrontal and frontal and has a medial border on the frontal and parietal. The anteromedial projection of the supratemporal lies between the postfrontal and parietal. The supratemporal is bordered medially by the parietal and postparietal and has a posterior border on the tabular. The staggered positions of the prefrontal, postfrontal and supratemporal relative to the midline series insure the structural strength of the skull. The postorbital is elongate and oval. It forms the posterior border of the orbit and has a sigmoid suture with the squamosal.

The maxillary and the anterior part of the jugal are curved in transverse section. The posterior part of the jugal gradually flattens out and the quadratojugal is flat in section. The maxillary forms the posterolateral margin of the external naris. Behind the naris, the maxillary is strongly indented by the nasal and shallowly indented by the prefrontal. The course of the maxillary-jugal suture is not entirely certain. The sculpture pattern of the holotype suggests that the jugal formed the entire lateral border of the orbit and extended forward to a suture with the prefrontal, excluding the maxillary from the orbit. The jugal extends far back of the orbit to a short suture with the quadratojugal and has a concave medial border on the postorbital. The exact location of the quadratojugal-squamosal suture is not known.

The squamosal is small compared with those of most other labyrinthodonts. It has two anterior projections, one between the jugal and postorbital and one between the postorbital and supratemporal.

The shape and sutural relations of the tabular are preserved on U.C.M.P. no. 61064. The tabular has a lateral border on the squamosal, an anterior border on the supratemporal and a medial border on the postparietal.

The lateral line system is inclosed in well-defined, shallow grooves about 2 mm. in width. The positions of all of the grooves with the exception of the transverse occipital groove are taken from the holotype. The supraorbital groove originates in the premaxillary, trends posterolaterally through the nasal and makes a right angle bend in the prefrontal. It then proceeds posteromedially into the frontal and makes another right angle bend and trends again posterolaterally. It joins the infraorbital and supratemporal grooves in the centre of the postorbital bone. The infraorbital groove begins near the premaxillary-maxillary suture and makes a slight medial bend in the anterior part of the maxillary. It then follows close to the lateral edge of the skull through the remainder of the maxillary and the anterior part of the jugal. In the centre of the postorbital portion of the jugal it turns upward sharply and runs transversely to the junction with the supraorbital and supratemporal grooves. The jugal groove begins at the sharp bend of the infraorbital groove and runs posteriorly to end just behind the jugal-squamosal suture. The supratemporal groove curves through the supratemporal bone and ends near the anterior edge of the tabular bone.

U.C.M.P. no. 61313, an impression of a posterolateral skull portion, is obviously derived from a very small individual of *D. kimberleyensis;* the cheek region lies at an angle to the skull table and the sutures of the tabular and postparietal bones are similar to those on the holotype. A distinct occipital groove runs transversely across the postparietal and tabular just within the occipital margin of the skull roof. The lateral terminations of the groove are not preserved.

A distinctive surface ornament covers the bones of the skull roof. It differs from both the pitted and the coarsely reticulate types of sculpture found on the skulls of most labyrinthodonts. The *Deltasaurus* pattern consists of a finely meshed web radiating from the centre of

each bone. The individual ridges are small and low in relief. The radial ridges are higher in relief than the concentrically arranged ridges, extend to the peripheries of each bone and tend to bifurcate distally. Rounded nodes on the radial ridges occur at points of bifurcation and at the points of junction with the concentric ridges. The concentric ridges divide the grooves between the radial ridges into small pits. Most of the bones of the skull roof are uniformly pitted over their entire surfaces. Certain small areas, especially the posterior portion of the nasal and the postero-lateral corner of the jugal, have only the radial ridges and lack the concentric ridges; the ridges of these areas are larger, better defined and more widely spaced than those of other parts of the skull.

The sculpture pattern of *Deltasaurus kimberleyensis* is basically similar to that of other members of the Rhytidosteidae. It is probably derived from the normal reticulate pattern by dimunition of the ridges and by emphasis on the radial components of sculpture.

The pits at the centre of each bone on the skull roof of the type specimen are larger than those near the edges, indicating that the original ossifications lay at the bone centres. Otherwise, there are no features on the sculpture pattern which are indicative of the growth of each bone. The bones are pitted over most of their surfaces, showing that the radial and concentric ridges were formed concomitantly in the growth of each bone. Similar pitting up to the margins of the tabular, postparietal and squamosal on the fragment of a very small skull, U.C.M.P. no. 61313, shows that this pattern characterizes early ontogenetic stages of *Deltasaurus kimberleyensis*.

This uniformity in the development of the sculpture pattern during growth is quite unlike the development of the reticulate type of sculpture as described by Bystrov (1935). In this type, the central pitted area of each bone represents the original ossification. With further growth a radiating pattern of ridges is formed about the original central pitted area. Transverse bars of ornament then develop between the ridges and gradually expand the central pitted area. Eventually the ridges and grooves will occupy only small rings with the bone peripheries.

Palatal surface of the skull (figs. 1b, 2a, 2b, 3b and 4b). The palate restoration (fig. 4b) is principally based on U.C.M.P. no 61063 (fig. 2a), a partial skull slightly smaller than the holotype. It consists of two fragments. The natural contact between the fragments is lacking but they are certainly derived from the same individual. They were found close together on the hill slope below V 6040 and the choanae and the anterior orbital borders are of identical size.

The bone of the dorsal surfaces is mostly weathered away, leaving an impression of its internal surface. A few scraps of bone remain in the region of the lateral border of the right orbit. The orbits resemble the holotype orbit in shape and position.

The palate surfaces were encased in hard matrix and are fairly well preserved. The larger fragment consists of the right side of the palate from the vomerine tusk to the quadrate region. It includes the internal naris and the sub-
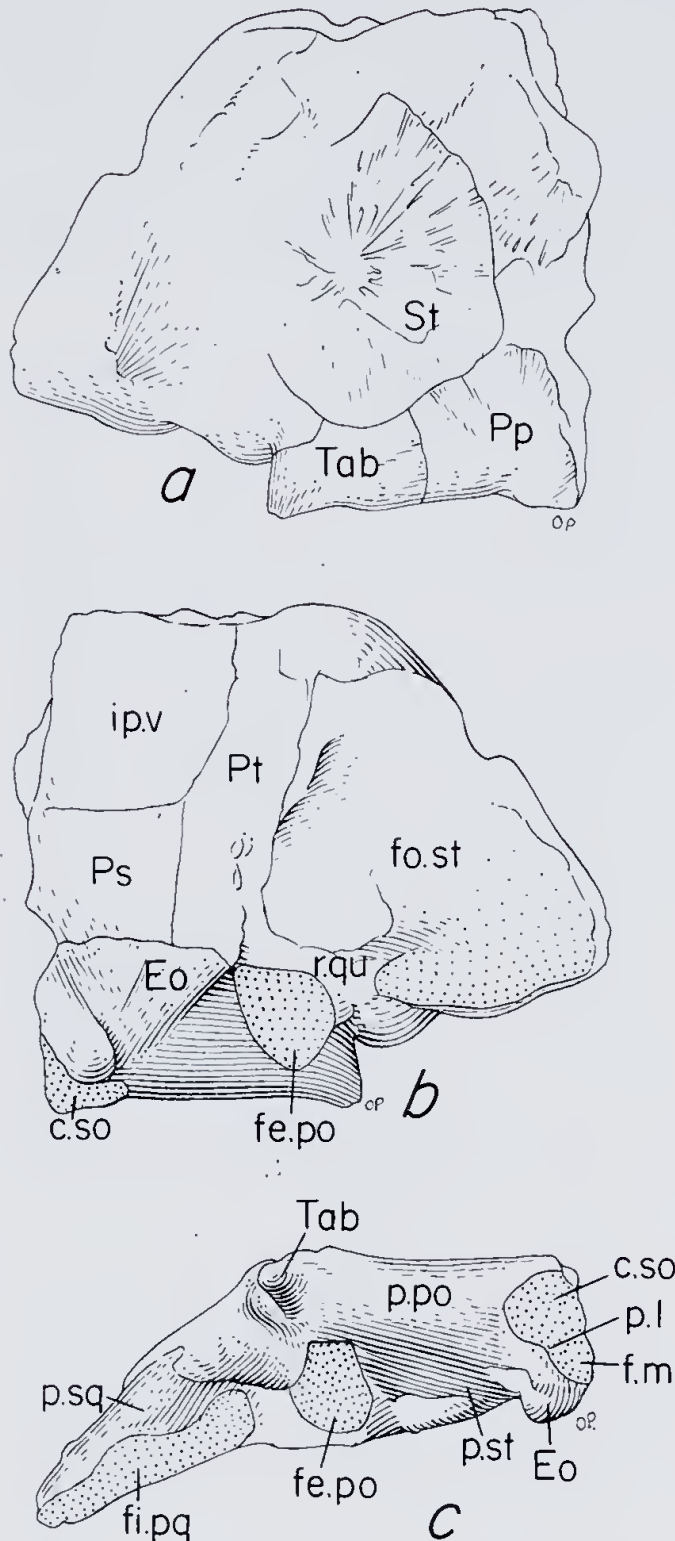

Fig. 3.—*Deltasaurus kimberleyensis* gen. et sp. nov., paratype U.C.M.P. no. 61064 (U.C.M.P. locality V 6040); skull fragment: a, dorsal view; b, palatal view; c, occipital view. All x 0.65.
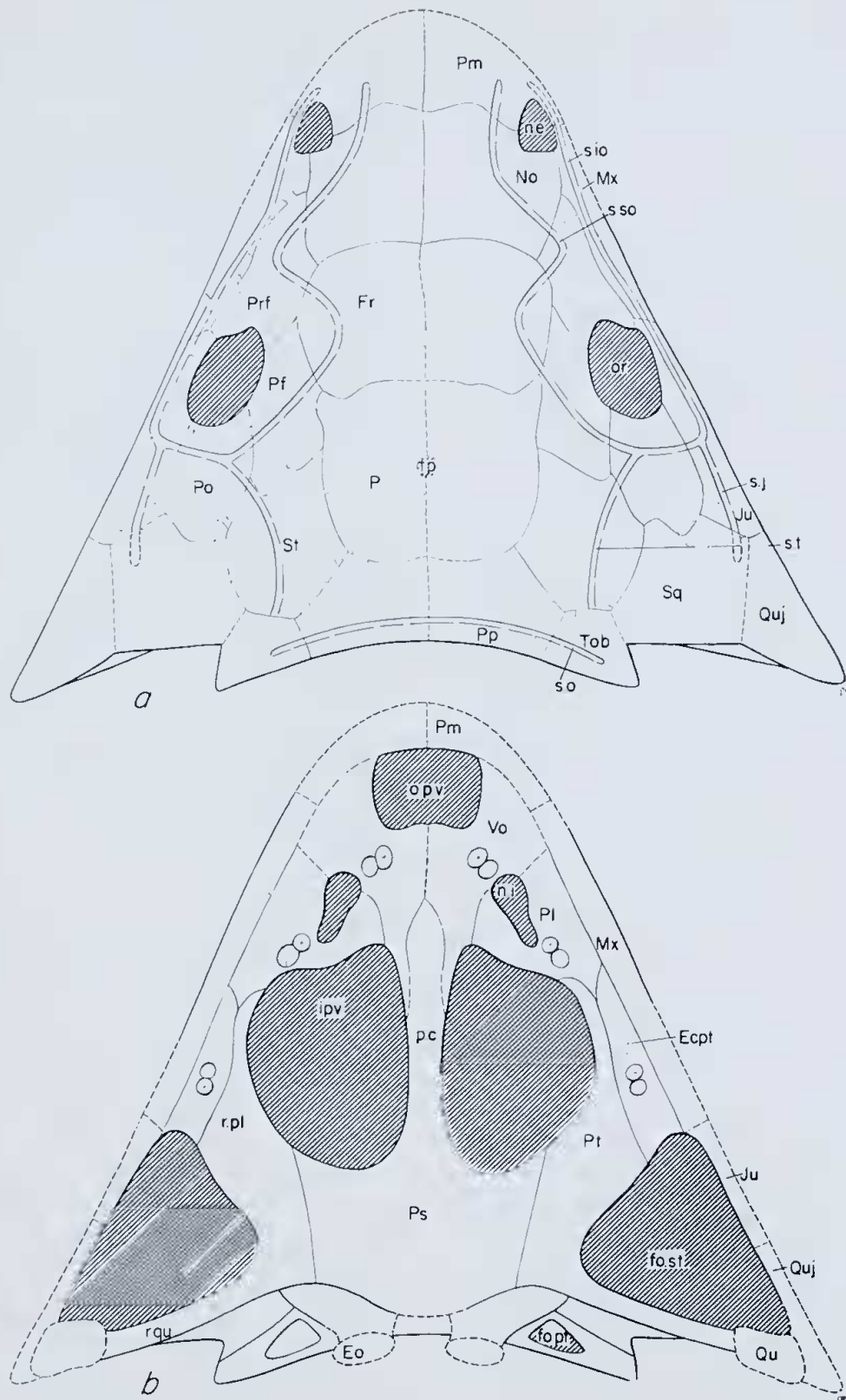
Fig. 4.—*Deltasaurus kimberleyensis* gen. et sp. nov., reconstruction of the skull, based mainly on W.A.M. no. 62.1.44, supplementary data from U.C.M.P. nos. 61062, 61064 and 61313: a, dorsal view; b, palatal view. x 0.33.

temporal fossa and also the anterior and lateral borders of the interpterygoid vacuity; some of the lateral edge is intact. The smaller left fragment has only the region about the internal naris and the anterior edge of the interpterygoid vacuity.

Four other specimens contributed the remainder of the palate restoration. The region anterior to the interpterygoid vacuity is based on the palate fragment of the holotype (fig. 1b). The orientation of the two fragments of U.C.M.P. no. 61063 indicates a broad, flat

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cultriform process of the parasphenoid; this is confirmed by U.C.M.P. no 61061 (fig. 2b), an isolated parasphenoid with scraps of the vomers still adhering to its anterior portion. The shape of the anterior part of pterygoid bone and the location of the pterygoid-parasphenoid suture are taken from the palate surface of the small posterolateral skull fragment, U.C.M.P. no. 61064 (fig. 3b). The quadrate ramus of the pterygoid is preserved on U.C.M.P. no 61062.

The various openings of the palate surface are relatively small compared with those of other Triassic labyrinthodonts.

The anterior palatal vacuity, preserved on the type, is unpaired and similar in shape to that found in most capitosaurids. It is twice as broad as long. The anterior and lateral borders are straight. The posterior border is bow-shaped with a median indentation.

The internal naris, best preserved on the left side of the U.C.M.P. no 61063, is pear-shaped with the apex at the posterior margin and the long axis is oblique both to the lateral edge of the skull and to the midline. It is farther from the lateral edge of the palate than in most other Triassic labyrinthodonts.

The short, broad interpterygoid vacuity occupies the central third of each side of the palate. The posterior and posterolateral borders are rounded. The medial border on the cultriform process is straight. The antero-lateral border is indented by the palatine bone.

The subtemporal fossa is broader than long. Its anterior border is nearly on a level with the posterior border of the interpterygoid vacuity. The posterolateral corner against the quadrate and quadratojugal bones is angular. The antero-medial border is indented by the usual "elbow" of the pterygoid.

The palatal surfaces of the premaxillary and maxillary bones are a few millimeters above the central palatal surface. The position of the premaxillary-maxillary suture and the posterior boundaries of the maxillary bone on the over-plating jugal bone are unknown.

Both fragments of U.C.M.P. no. 61063 bear a portion of the marginal tooth row. The actual teeth have been leached away, leaving only hard cores of matrix that retain the shapes of the pulp cavities. Each core has a central pillar surrounded by radially arranged spokes that represent the hollow spaces within the labyrinthine folds of the original dentine. The internal cores reflect the shapes of the original teeth. They are of uniform height, about 4mm. Some lie close together and others are separated by empty sockets. They are anteroposteriorly compressed and resemble the teeth of other labyrinthodonts in this respect.

The quadratojugal-jugal suture is placed with reference to the course of this suture on the dorsal surface of the holotype. The quadrato-jugal of the holotype extends to the postero-lateral skull corner and obviously covered the lateral surface of the quadrate; the quadrato-jugal-quadrate suture is placed accordingly on the palate reconstruction.

Internal to the premaxillary and maxillary lie the vomer, palatine and ectopterygoid, each bearing a large tusk flanked by a replacement pit. There are no rows of smaller teeth running between the large tusks parallel to the marginal tooth row.

The vomer extends from the posterior and lateral borders of the anterior palatal vacuity to the anteromedial border of the interptery-goid vacuity. U.C.M.P. no. 61061 (fig. 2b) shows that the vomer sheathed the antero-lateral edge of the cultriform process at least as far posteriorly as indicated in figure 4b. Part of the vomer-parasphenoid suture and part of the intervomer suture are preserved on U.C.M.P. no. 61063. Anterolaterally the vomer borders the maxillary and probably also had a short suture with the premaxillary. The vomer-palatine suture of U.C.M.P. no 61063 runs anterolaterally from the forward edge of the interpterygoid vacuity and becomes indistinct between the choana and the vomerine tusk. It probably curves laterally to end at the forward edge of the choana.

The palatine separates the maxillary from the internal naris and meets the vomer lateral as well as medial to the naris. In other labyrintho-donts the maxillary has a medial extension which forms the lateral border of the internal naris and which has a posterior suture with the palatine and an anterior suture with the vomer. The palatine is bordered by the pterygoid and ectopterygoid posteriorly. The palatine tusk and replacement pit are immediately behind the internal naris.

The ectopterygoid is an elongate bone. The tusk and replacement pit are near the centre of its length.

The anterior part of the pterygoid is strongly developed and the sutural contact with the palatine is extensive for a Triassic genus. The central portion between the parasphenoid bone and the subtemporal fossa is unusually narrow. The quadrate ramus is long and slender.

The body of the parasphenoid is exceptionally broad compared with the width of the central portion of the pterygoid bone. It is bounded posteriorly by oblique sutures with the exocci-pitals and probably had a short free margin between the condyles.

The broad flat cultriform process of the para-sphenoid extends forward between the inter-pterygoid vacuities and terminates between the vomers as a conical projection. It is slightly constricted in width opposite the centres of the interpterygoid vacuities.

A few scraps of the right exoccipital adhere to the posterior edge of the palate of U.C.M.P. no. 61064. The exoccipital-parasphenoid suture is not preserved but the bone grain indicates that the exoccipital contribution to the palatal surface must have been small. The condyles are restored after *Peltostega erici* (Nilsson, 1946, fig. 6).

The quadrate condyle of the reconstruction is completely conjectural.

A dense shagreen of small teeth completely covers most of the palate. The original dentine of these teeth has been leached away leaving only labyrinthine casts of the pulp cavities. The

shagreen covers all of the bone surface anterior and lateral to the interpterygoid vacuities. It even extends over the palatal surfaces of the maxillary bone, both medial and lateral to the marginal tooth row. U.C.M.P. no. 61061 shows that the shagreen covered the surface of the cultriform process of the parasphenoid close to its base. It probably extended onto the corpi of the parasphenoid and pterygoid.

The denticles vary in size over the palate. Those on the anterior part of the cultriform process are twice as large as those on the palatine and vomer at the anterior edge of the interpterygoid vacuity.

Occipital surface of the skull (figs. 2c, 3c and 5). U.C.M.P. nos. 61062 (fig. 2c) and 61064 (fig. 3c) are left posterolateral skull corners broken off slightly lateral to the midlines. The first, derived from a skull comparable in size to the holotype, is uncrushed and retains much of the actual shape of the occiput. The second, derived from a smaller skull, has undergone considerable dorsoventral compression. The restoration of the occiput (fig. 5) is a composite of both of these. Both are fairly complete in the central and lateral portions of the occiput but lack the occipital and quadrate condyles. The occipital structures are preserved mainly as internal impressions with a few scraps of bone adhering in places.

The angular occipital margin of the skull roof of U.C.M.P. no 61062 closely matches that of the holotype. The skull table is flat. The cheek margin descends ventrolaterally, forming a 40 degree outside angle with the skull table at the otic notch. The lower half of the cheek margin is set at a 25 degree outside angle with the upper half. The ventral margin of the occiput of this specimen is slightly convex upward and the missing quadrate region was below the level of the parasphenoid bone.

The postparietal, tabular and squamosal of U.C.M.P. no. 61062 are produced backward into a short ledge overhanging the occipital structures. The quadratojugal probably had a similar ledge but this is not preserved. The postparietal-tabular and the tabular-squamosal sutures are placed on the ledge according to their positions on the skull roofs of the holotype and U.C.M.P. no 61064.

The paraoccipital process of the tabular is preserved as internal impression on both occipital fragments. The pattern of bone grain on U.C.M.P. no 61064 shows the approximate position of the tabular-exoccipital suture.
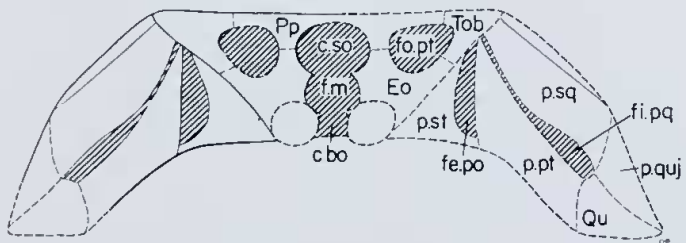

Fig. 5.—*Deltasaurus kimberleyensis* gen. et sp. nov., reconstruction of the occipital surface of the skull, based on U.C.M.P. nos. 61062 and 61064; size based on no. 61062. x 0.38.

The supraoccipital process of the postparietal was a short cylindrical structure. A vertical groove filled with splintery bone is all that remains of this process on the occiput of U.C.M.P. no. 61064. The position of the suture with the underlying exoccipital bone is unknown.

The exoccipitals of both specimens are badly damaged but each contributes some information. The paraoccipital and vertical processes of both diverge in the usual manner from the upper part of the main body of the bone. The broken bases of the condyles are marked by radiating bone grain. The condylar base of U.C.M.P. no. 61062 is just above the level of the parasphenoid bone. U.C.M.P. no. 61064 retains a processus lamellosus on the medial side of the vertical process. A long palatal process of the exoccipital is present on both specimens. It remains in natural position on U.C.M.P. no. 61062 where it runs ventrolaterally to a contract with the pterygoid bone. The processus basalis and vagus foramen are not present on either specimen.

The impression of a large triangular plate of bone is laterally continuous with the edge of the paroccipital process of U.C.M.P. no. 61064. The apex of this plate lies near the exoccipital-tabular suture and the broad base rests on the upper surface of the palatal process of the exoccipital. It has a flat posterior surface and a straight lateral edge. It slopes downward, inward and forward on this specimen; a few scraps of impression remaining on the inner side of the paraoccipital process of U.C.M.P. no. 61062 indicates that the plate of bone originally lay in a more dorsoventrally orientated plane as its ventrolateral corner lies near the exoccipital-pterygoid suture. This plate has the morphologic position of a subotic process of the exoccipital. The fenestra ovalis of cyclotosaurids is situated just anterior to and just medial to the posterior edge of the exoccipital-pterygoid suture; the posterior and ventral margins of this foramen are formed by the subotic process. If the identification is correct, the subotic process of *D. kimberleyensis* is peculiar. In all other Triassic labyrinthodonts for which it has been reported it is a short cylindrical process just ventrolateral to the condyle.

The posttemporal fossa of U.C.M.P. no. 61062 is an oval depression, enclosed by the paraoccipital bar, the vertical process of the exoccipital and the overhanging ledge of the skull roof. The dorsal, medial and lateral margins are well-defined; the ventral margin is less distinct.

The large opening in the center of the occiput was undoubtedly tripartite as in other labyrinthodonts. The lateral borders of the supraoccipital foramen and the foramen magnum, divided by the processus lamellosus lamellosus, are present on U.C.M.P. no. 61064. The shape of the basioccipital foramen is unknown because the processus basalis which delimits the lower edge of the foramen magnum is not preserved. The large supraoccipital foramen is broader and perhaps higher than the foramen magnum. The supraoccipital and basioccipital were probably cartilaginous as in other late

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labyrinthodonts; no traces of ossification were found in the supraoccipital foramen.

The ascending process of the pterygoid, preserved as an internal impression on the occipital surface of U.C.M.P. no. 61062, is perpendicular to the quadrate ramus and is broken off just medial to the missing quadrate bone. The flat external surface extends anteromedially from the broken lateral edge and ends with an indistinct medial margin under the otic notch. The process is highest in its most medial portions and gradually decreases in height laterally.

The descending process of the squamosal and quadratojugal are poorly preserved on both specimens. The sinuous ventral margin on the processes, shown in the reconstruction, is principally based on U.C.M.P. no. 61064. The suture between the squamosal and quadratojugal is hypothetical.

U.C.M.P. no. 61062 retains the very indistinct outlines of a narrow palatoquadrate fissure between the lateral portions of the occipital processes of the squamosal and pterygoid. The smooth lower margin of the squamosal on U.C.M.P. no. 61064 indicates that this bone was not in sutural contact with the pterygoid for most of its length and that the palatoquadrate fissure was even more extensive than is indicated by U.C.M.P. no. 61062.

The pteroccipital fenestra is a large opening between the ascending process of the pterygoid and the lateral edge of the subotic process of the exoccipital. The shape of the fenestra is reconstructed from both occipital surfaces.

Measurements. Estimates of the original dimensions of the type skull are:

Skull roof

Median length	22.2 cm.
Median length from the snout tip to the level of the posterior borders of the external nares	5.2 cm.
Median length from the level of the posterior borders of the external nares to the level of the anterior borders of the orbits	6.0 cm.
Median length from the level of the anterior borders of the orbits to the level of the posterior borders of the orbits	3.6 cm.
Median length from the level of the posterior borders of the orbits to the posterior edge of the skull roof	7.6 cm.
Width across the posterior borders of the external nares	10.8 cm.
Width across the posterior borders of the orbits	20.0 cm.
Width across the posterolateral skull corners	29.4 cm.
Least interorbital width	11.3 cm.

Palatal surface

Median length	21.4 cm.
Median length from the snout tip to the level of the anterior borders of the interpterygoid vacuities	8.4 cm.
Median length from the level of the posterior borders of the interpterygoid vacuities to the posterior edge of the palate	5.0 cm.
Greatest length of the left interpterygoid vacuity	8.0 cm.
Greatest width normal to the length of the left interpterygoid vacuity	5.7 cm.
Length of the anterior palatal vacuity	2.7 cm.
Width of the anterior palatal vacuity	3.8 cm.
Length of the left internal naris	2.7 cm.
Greatest width normal to the length of the left internal naris	1.2 cm.

The lower jaw (figs. 6-8). Lower jaw fragments of *Deltasaurus kimberleyensis* are the most abundant fossils in the Blina collection. Most of these were found in the quarries and about the slopes at V 6040. One was collected at the Noonkanbah locality, V 6044 and four are from the B.M.R. locality (Dry Corner). A pair of articulated rami, U.C.M.P. no 61098 (fig. 6a), was found in the quarry at V 6043 only a few feet from articulated jaws of a brachyopid. This specimen closely matches the skull outline of *D. kimberleyensis* and is certain to pertain to the same species; the numerous fragmentary jaws are referred through comparison with this specimen.

The articulated jaws and many of the partial jaws are largely internal casts of the region anterior to the glenoid fossa. They compositely show the shape of the adductor fossa and of the meckelian space anterior to it. A comparative review of the more promising of the internal casts has revealed the courses of many of the deep sutures of the dermal bones. In many instances fossae and fenestrae are preserved as infillings of matrix that project from the surfaces of the casts. Scraps of the original enclosing cylinders of dermal bone adhere to a few of the casts.

Four of the jaw fragments, U.C.M.P. nos. 61100, 61114, 61119 (fig. 6c) and 61122 (fig. 6k) preserve portions of the retroarticular processes. The surface bone has been leached from the dorsal, lingual and labial sides of these, exposing the cores of the surangular bones in the retroarticular processes and of the articular bones beneath the glenoid fossae.

W.A.M. no. 60.9.16 retains part of the external labial surface and five additional specimens, U.C.M.P. nos. 61071 (fig. 6h), 61104, and 61125, and B. M. R. nos. F21805 and F21807 include impressions of parts of this surface. These show the character of the external ornament and the positions of several of the sutures. A portion of the external lingual surface is preserved on U.C.M.P. no. 61121 (fig. 6b).

The restoration technique is that developed by Nilsson (1943). A composite restoration was made of each aspect of the internal cast of the lower jaw (figs. 7a, b and c), utilizing the internal cast specimens and the retroarticular cores. The gross outlines and proportions are based on U.C.M.P. no. 61096. A second series of retorations (figs. 8a, b and c), built about the first series, shows the external surfaces of the lower jaw. Approximately 2.0 mm. have been added to all surfaces to allow for the thickness of the dermal bone. The symphysial region of the articulated jaws, the labial impressions and the lingual fragment have contributed to the external restorations. Unknown external sutures are placed according to the general labyrinthodont arrangement of the dermal bones of the lower jaw described by Nilsson (1943). The composite internal cast will be considered first and will be followed by a description of the restored external surfaces.
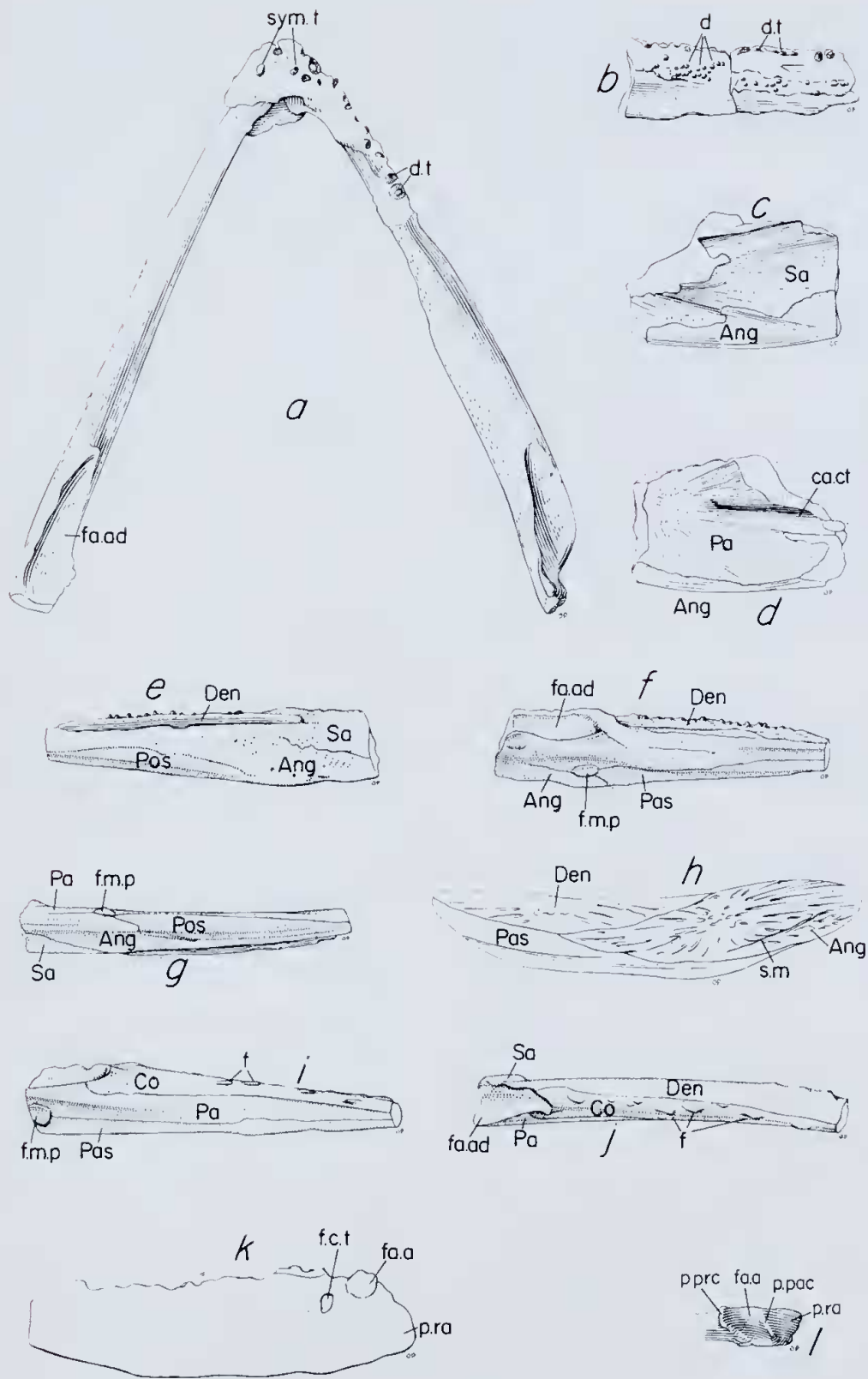
Fig. 6.—*Deltasaurus kimberleyensis* gen. et sp. nov., paratypes: a, U.C.M.P. no.
61098 (U.C.M.P. locality V 6043), lower jaw, dorsal view; b, U.C.M.P. no. 61121
(U.C.M.P. locality V6042), lower jaw fragment, lingual view; c, U.C.M.P. no. 61119
(U.C.M.P. locality V 6040), lower jaw fragment, labial view; d, the same, lingual
view; e, U.C.M.P. no. 61101 (U.C.M.P. locality V 6040), lower jaw fragment, labial
view; f, the same, lingual view; g, the same, ventral view; h, U.C.M.P. no. 61071
(U.C.M.P. locality V 6040), latex peel of the external impression of the labial sur-
face of a lower jaw fragment; i, U.C.M.P. no. 61099 (U.C.M.P. locality V 6042),
lower jaw fragment, lingual view; j, the same, dorsal view; k, U.C.M.P. no. 61122
(U.C.M.P. locality V 6040), lower jaw fragment, lingual view; l, U.C.M.P. no. 61068
(U.C.M.P. locality V 6040), articular facet of a lower jaw, dorsal view. All x 0.43.

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In dorsal view (fig. 7a) each internal cast is slightly convex labially. It is narrowest at the symphysis and gradually increases in width back to the glenoid fossa. The retroarticular process tapers to a pointed apex. The upper surface, anterior to the adductor fossa, is occupied by the internal impressions of the dentary and coronoid bones. There are presumably three bones in the coronoid series as in other labyrinthodonts but the sutures dividing these were not found in the collection. The dentary-coronoid suture runs obliquely across the upper surface from a lingual point just behind the symphysis to a labial point lateral to the anterior edge of the adductor fossa. The coronoid ends at the adductor fossa; the dentary continues back to overlap a portion of the surangular impression on the labial surface of the jaw. The dentary impression on the dorsal surface is flat; the coronoid impression is convex. U.C.M.P. nos. 61099 (figs. 6i and j) and 61088 are cylindrical projections on the coronoid internal impressions; these are probably infillings of foramina that carried blood and nerve supply to the bone and teeth.

The adductor fossa has a flattened posterior border against the articular and a bluntly pointed anterior border.
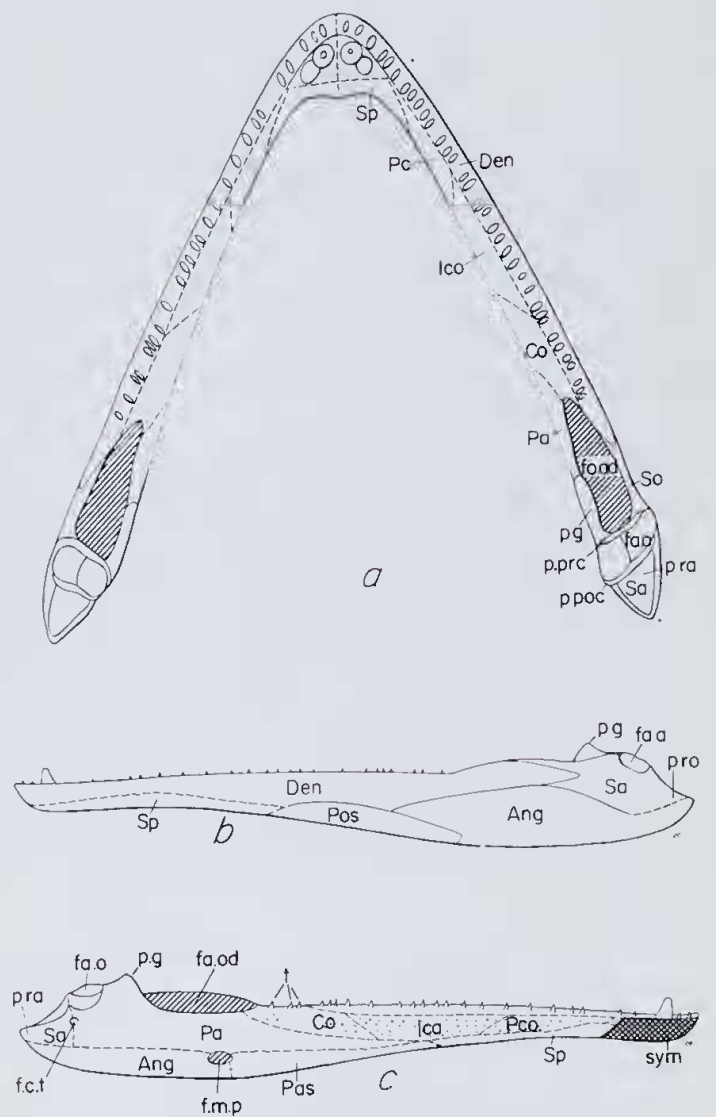

Fig. 8.—*Deltasaurus kimberleyensis* gen. et sp. nov., reconstruction of the external surfaces of the dermal bones of the lower jaw; size based on U.C.M.P. no. 61098; outlines based on the reconstructed internal cast, with compensation for the thickness of the dermal bones: a, dorsal view, supplementary data from U.C.M.P. nos. 61068 and 61121; b, labial view, supplementary data from U.C.M.P. nos. 61068 and 61071; c, lingual view, supplementary data from U.C.M.P. nos. 61068 and 61121. All x 0.34.

The glenoid facet (fig. 6l) is formed by the articular bone encased by the surrounding surangular. It is divided by a low longitudinal crest. Precondylar and postcondylar processes bound the facet fore and aft. The precondylar process is lingually continuous with the high rounded hamate process of the prearticular bone. The hamate process lies along the posterior lingual border of the adductor fossa and perhaps served as an insertion area for part of the adductor muscle mass.

The dorsal aspect of the retroarticular process is triangular. It is occupied by the shallow insertion area of the m. depressor mandibulae.

In labial aspect (fig. 7b), the internal cast gradually deepens posteriorly from the symphysial region. The upper surface, anterior to the adductor fossa, is flat. The labial wall of the adductor fossa is high and rounded. The anterior half of the lower border is flat; the posterior half is convex ventrally.

Fig. 7.—*Deltasaurus kimberleyensis* gen. et sp. nov., reconstruction of the internal surfaces of the dermal bone of the lower jaw; size based on U.C.M.P. no. 61098; a, dorsal view, based principally on U.C.M.P. nos. 61068, 61098, 61099, 61101 and 61122; b, labial view, based principally on U.C.M.P. nos. 61068, 61101, 61119 and 61122; c, lingual view, based principally on U.C.M.P. nos. 61099, 61101, 61119 and 61122. All x 0.38.

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The impressions of the surangular, angular, dentary and splenial bones cover the labial surface. Several specimens have contributed portions of the angular-surangular and angular-dentary sutures. The surangular covers a large area on the dorsoposterior portion of the jaw and includes all of the retroarticular process. Anterodorsally the surangular bears a longitudinal groove for the splinter-shaped posterior process of the dentary. The dentary covers most of the lingual surface anterior to the adductor fossa. It is bordered ventrally by the splenial and postsplenial. The angular fills the area below the surangular and the dentary and behind the postsplenial.

The lingual surface of the internal cast of the lower jaw (fig. 7c) is similar to the labial surface in outline except around the border of the adductor fossa, which is produced into the high, rounded hamate process posteriorly and is lower than the lateral border anteriorly.

The prearticular extends far forward on the lingual surface between the splenials and coronoids, tapering to a fine point not far behind the symphysial region. The suture between the prearticular and surangular is unknown; it probably descends more or less vertically from the glenoid facet as in other labyrinthodonts.

The most anterior portions of the lingual surface of the internal cast are not represented in the collection. The coronoid series tapers forward and probably terminates as a sharp point just behind the symphysis. The internal cast within the symphysial region was probably covered by dentary impression above and splenial impression below.

The posterior meckelian foramen, well defined on several internal casts, is unusually small for a Triassic genus. It is only 7mm wide and 4mm deep on U.C.M.P. no. 61101 (fig. 6f), a jaw fragment slightly larger than U.C.M.P. no. 61068. The prearticular forms its upper border and the angular and postsplenial its ventral border.

The lingual surface of U.C.M.P. no. 61119 (fig. 6d) retains the deeper layers of the prearticular bone. These contain a shallow longitudinal groove just below the glenoid facet which is probably the internal wall of the chorda tympani canal. Near the center of the adductor fossa this groove becomes indistinct. The chorda tympani canal probably opened through a foramen into the adductor fossa and the nerve probably continued forward from this foramen through the meckelian space.

In ventral view the internal cast of the lower jaw is sharply keeled from the retroarticular process to the posterior part of the postsplenial. The central part of the lower surface is rounded. The ventral surface of the symphysial region is flat.

The shapes of the reconstructed external surfaces closely resemble those of the internal cast except in the symphysial region.

The symphysial region is nearly complete on U.C.M.P. no. 61098. The dentaries and splenials expand inwardly into a broad triangular plate. The dentaries form the dorsal surface of this plate and the splenials the ventral surface. The dentary surface of this plate carries sym-

physial tusks internal to the marginal tooth row. The surface surrounding the tusks is covered with a shagreen of small denticles identical with those of the palate.

Remnants of dermal bone adhere to the dorsal surfaces of U.C.M.P. nos. 61101 (figs. 6e and f) and 61121 (fig. 6b). These carry a few internal cores of the marginal teeth of the dentary which resemble those of the maxillary row in size, shape and spacing. Remnants of the coronoid series of W.A.M. no 60.9.16, U.C.M.P. nos 61121 and 64972 and B.M.R. no. F21817 display a shagreen of denticles which are identical with those of the palatal surface of the skull and those of the symphysial plate. A reasonable interpretation from these specimens is that the coronoid series was completely covered with shagreen.

No suture between the dentary and the coronoid could be distinguished on the shagreened areas of the specimens mentioned above, which suggests that the dorsal surface of the dentary is confined to the narrow strip which carries the dentary tooth row. If this interpretation is correct the coronoid bones have a considerably larger area on the external surface than they have on the internal cast and must overlap the dentary with a squamous suture. This condition is the reverse of the situation in *Aphaneramma rostratum* (Nilsson, 1943, figs. 4A and 4B) where the dentary overlaps the coronoid series and the superficial surface of this bone is larger than its internal impression.

Impressions of the external surfaces of the angular and postsplenial are preserved on latex positives of U.C.M.P. nos. 61104, 61071 (fig. 6h) and 61125 and B.M.R. no. F21807. The superficial surfaces of these bones are considerably larger than their deep surfaces. The angular must overlap extensively on the external surface of the surangular and slightly on the external surface of the dentary and the postsplenial must overlap extensively on the external surfaces of both the angular and the dentary. The postsplenial terminates posteriorly as a sharp projection over the angular. These squamous relationships are consistent with the observation of Nilsson (1943) on the Spitzbergen trematosaurs. The splenial bone of *D. kimberleyensis*, not preserved in the collection, probably also had a larger superficial than deep surface.

The ornament pattern of the angulars and postplenials, as displayed on the latex impressions, is identical with that of the skull roof.

U.C.M.P. no. 61071 shows the diagonal course of the mandibular lateral line groove on the angular bone. It descends anteroventrally from the glenoid region. The oral and accessory grooves of the lower jay, if present, are not preserved.

The superficial sutures of the lingual surface (fig. 8c) are hypothetical. The reconstruction is based on the squamous relationships of the dermal bones of this surface described by Nilsson. If the same relationships maintain in D. kimberleyensis, the angular, postsplenial, splenial and coronoid bones all have larger superficial than deep surfaces and all extensively

overlap the external surface of the prearticular bone.

The lower jaw of *D. kimberleyensis* has the basic temnospondyl construction. It shares a well developed retroarticular process with most other Triassic genera of this group. The strong development of the hamate process parallels the Cyclotosauridae. The distinctive feature of the lower jaw of *D. kimberleyensis* are the expanded symphysial plate, the small size of the posterior meckelian foramen and the shagreen of denticles which covers the coronoid bones and the symphysial portion of the dentary bone.

Measurements. Estimates of the original dimensions of the lower jaw, U.C.M.P. no. 61098 are:

Length (outside curvature) from the symphysis to the tip of the retro-articular process	21.7 cm.
Length (outside curvature) from the symphysis to the forward edge of the adductor fossa	13.9 cm.
Length of the symphysis	2.6 cm.
Length of the adductor fossa	4.2 cm.

Dermal shoulder elements (fig. 9). Ten clavicular and nine interclavicular fragments are referred to *D. kimberleyensis*. All but one of these are external surfaces which bear delicate sculpture patterns identical to that of the holotype. The odd fragment is a detached cleithral process of the clavicle; the base of this process closely matches the broken bases of two of the clavicular fragments. The visceral surfaces of the dermal shoulder girdle are not known.
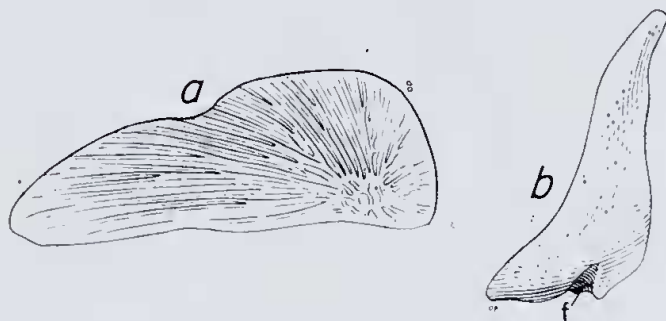
Fig. 9.—*Deltasaurus kimberleyensis* gen. et sp. nov., paratypes; a, U.C.M.P. no. 61092 (U.C.M.P., locality V 6043) right clavicle, ventral view; b, U.C.M.P. no. 61082 (U.C.M.P. locality V 6040), left cleithral process of clavicle, lateral view. x 0.77.

U.C.M.P. no. 61092 (fig. 9a), the external impression of the ventral surface of a left clavicle, is about 7.0 cm. in greatest length (along the lateral edge). The outlines are complete except for a small piece broken from the medial edge. The medial and posterior borders are convex. The lateral border is sinuous. The sculpture pattern is reflected on a latex peel of this impression; the centre of ossification, marked by a few small pits, lies just medial to the shallow notch near the posterior end of the lateral edge; the remainder of the surface is covered with a spiral pattern of fine bifurcating ridges which curve out from the ossification centre in a counter-clockwise direction.

The cleithral process (U.C.M.P. no. 61082, fig. 9b) rests on the postero-lateral corner of the ventral surface. The tip of the process is

inclined posteriorly. The upper edge of a foramen, probably for circulatory supply, is present on the base.

The interclavicular specimens are all too fragmentary for accurate description. Several of these, however, suggest that the posterior portion of the bone was a broad, diamond-shaped plate as in other Triassic labyrinthodonts.

Deltasaurus pustulatus, sp. nov.
(figs. 10 and 11)

Holotype. B.M.R. no. F21775, a partial skull roof with a small fragment of the palate surface and matching impression of the skull roof.

Type locality. Beagle Ridge Bore (B.M.R. 10), Kockatea Formation, South-West Division, Western Australia. The skull roof and its impression are preserved on the two surfaces of a break through core no. 28 (2614′-2624′). The core is 8.6 cm in diameter and composed of a uniform grey-green shale.

Diagnosis of the species. A *Deltasaurus* with bone sculpture composed principally of rows of pustules which radiate out from bone centers, with no pitting or concentric ridges. External naris with angular posterior border. Skull relatively narrower than that of *Deltasaurus kimberleyensis*.

Description. The ventral surface of the break carries the skull roof. A large piece is missing,
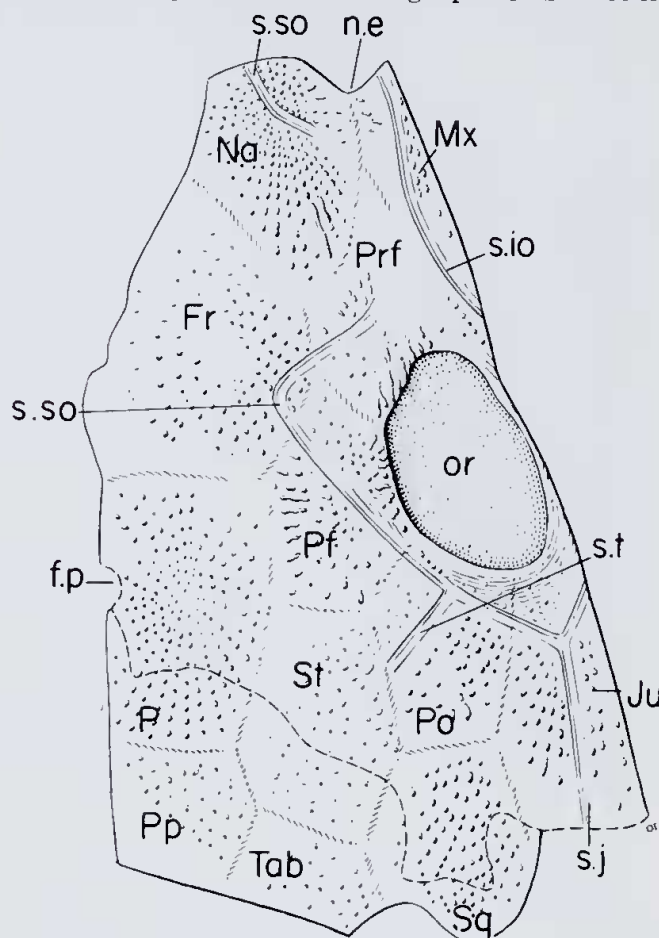

Fig. 10.—*Deltasaurus pustulatus* sp. nov., holotype, B.M.R. no. F 21775 (Beagle Ridge Bore); composite illustration of the skull roof and its external impression; the dashed line across the posterior part of the illustration is the edge of the actual specimen; the areas behind this dashed line are preserved only as impression. x 1.3.

probably spalled away during drilling operations, and the specimen was originally more complete medially and posteriorly. On the medial side the broken edge of the skull coincides with the median side of the parietal bone and the posterior half of the frontal bone; the broken edge then bends laterally and passes through the frontal and nasal bones. The broken posterior edge of the skull roof runs irregularly through the center of the postorbital region. A portion of the internal cast of the skull roof is preserved behind the broken posterior edge. Sutural impressions could not be identified on this internal cast. The specimen terminates anteriorly near the posterior border of the external naris against the rim of the core. The lateral edge of the skull roof is intact from the external naris to the posterior edge of the jugal bone.

An X-ray photograph shows a section of the alveolar border of the maxillary bone along the lateral edge of the skull roof. It is only a few millimetres broad and extends from a point 1.8 cm posterior to the orbit to a point 1.3 cm anterior to the orbit. The anterior part of the process had broken loose from the edge of the skull and shifted medially. A row of maxillary teeth, faintly discernable on the X-ray, runs the length of the process. Preparation of the palatal surface through the base of the core is not advisable as this small piece of maxillary is the only part of the palatal structures preserved and as the skull roof is exceedingly thin and fragile.

The polished edge of the core shows two anterior teeth in cross-section. The lateral one is a marginal tooth of the maxillary row and the medial one appears to be a vomerine tusk. The presence of this latter tusk implies a piece of vomer bone to underlie and support it but such a fragment was not observed on the X-ray.

The upper surface of the split core carries the external impression of the skull roof with a few scraps of bone adhering to it. It includes
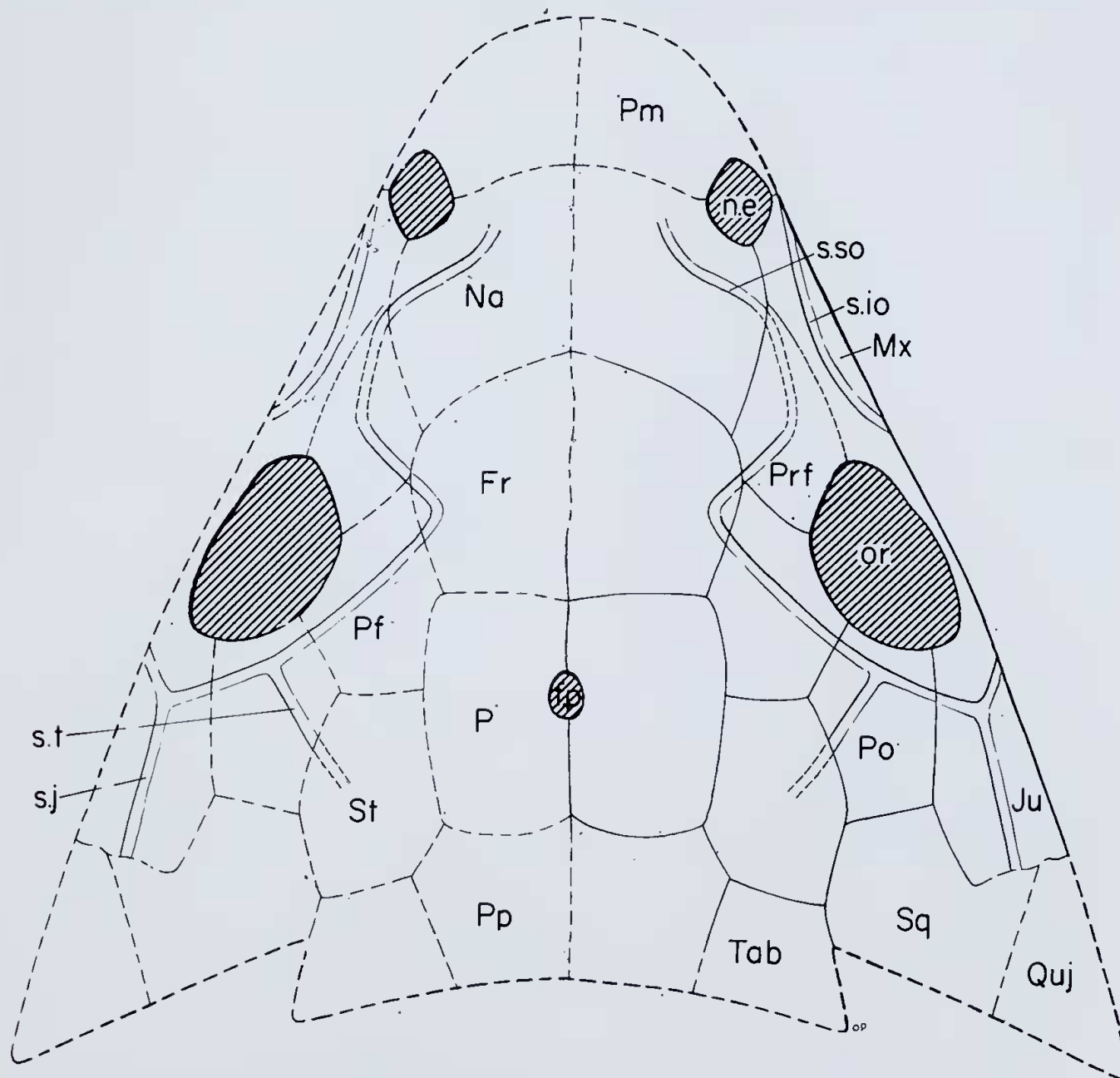

Fig. 11.—*Deltasaurus pustulatus* sp. nov., composite reconstruction of the dorsal surface of the skull based on the skull roof, B.M.R. no. F 21775, and its external impression   x 1.33.

the impression of a posteromedial portion of the skull roof which has been lost from the actual specimen.

The orbital margins and portions of the borders of the external naris and parietal foramen are clearly marked on both surfaces. The surface sculpture and the grooves of the lateral line system are well preserved on the skull roof. The sutures are more clearly indicated on the impression.

The orbit has a flattened lateral border, an angular anterior border and rounded medial and posterior borders. It lies close to the lateral edge, level with midline center of the reconstructed skull.

The posterior border of the external naris is angular.

The parietal foramen, unknown in *D. kimberleyensis,* lies within the anterior half of the medial suture of the parietal bones.

The external impression includes the complete parietal, supratemporal, postorbital, postfrontal and jugal bones and portions of the nasal, frontal, postparietal, squamosal, maxillary and tabular bones. The premaxillary and quadratojugal are entirely lacking. The arrangement of the bones on the skull roof is quite similar to the arrangement in *D. kimberleyensis.* Further description at this point is not necessary as minor variations will be considered in the following comparative section.

The sculpture is delicate and regular. Rows of small round pustules radiate out from the center of each bone. The pustules are small and indistinct at the center of each bone and become progressively larger and more sharply defined towards the peripheries. There are no pits and rudimentary ridges can be observed only in the posterior part of the nasal bone.

The portions of the supraorbital, infraorbital, jugal and supratemporal grooves which are preserved on the specimen are similar to those of *D. kimberleyensis* in shape and position. They are concentrated in the lateral part of the skull roof. The entire course of the supraorbital groove, with the exception of the part lying on the prefrontal, may be traced. The infraorbital groove is present on the maxillary anterior to the orbit and on the jugal and postorbital posterior to the orbit. The anterior part of the jugal groove is well-marked. The supratemporal groove is distinct on the postorbital and ends abruptly at the postorbital-supratemporal suture. The portions of the tabular and postparietal which would carry the occipital groove if present, are not preserved.

Measurements. Estimates of the original dimensions of the skull roof are:

Median length	9.3 cm.
Median length from the snout tip to the level of the posterior borders of the external nares	2.1 cm.
Median length from the level of the posterior borders of the external nares to the level of the anterior borders of the orbits	2.1 cm.
Median length from the level of the anterior borders of the orbits to the level of the posterior borders of the orbits	1.9 cm.
Median length from the level of the posterior borders of the orbits to the posterior edge of the skull roof	3.2 cm.
Width across the posterior borders of the external nares	4.4 cm.
Width across the posterior borders of the orbits	7.8 cm.
Width across the posterolateral skull corners	10.8 cm.
Least interorbital width	4.6 cm.
Diameter of the parietal foramen	0.5 cm.

Comparison of *Deltasaurus pustulatus* with *Deltasaurus kimberleyensis*

The well core specimen is congeneric with *D. kimberleyensis* of the Blina Shale. The bones of the skull roof and the system of sensory grooves are generally similar to those of the Blina species. There is no lacrimal bone. The bones bordering the median suture are considerably larger than those of the lateral portions of the skull. The orbit has a somewhat flattened lateral border and a pointed anterior border and is placed close to the lateral edge of the skull.

The most important distinction of the Kockatea skull roof and the one which clearly necessitates a specific separation from the Blina form lies in the character of the surface sculpture. The sculpture pattern of *D. pustulatus* is comparatively simple. There are no concentric ridges, and, consequently, no pits. Only a few radiating ridges are present. The pustules apparently correspond to the nodes along the radiating ridges of *D. kimberleyensis* pattern in which the radiating and concentric ridges have been supressed and the nodes have been emphasized. The difference is not ontogenetic. The sculpture on a fragment of a very small skull of *D. kimberleyensis* (U.C.M.P. no. 61313) from V 6040 is recognizable as an early stage of the sculpture found on the holotype of *D. kimberleyensis.* The pits are well-developed but small and the radiating ridges, although present, are not as pronounced as those on the holotype.

The skull of *D. pustulatus* is narrower than that of *D. kimberleyensis.* The width across the posterior borders of the orbits of the restored skull roof of *D. pustulatus* is 0.839 of the estimated median length. The same index in *D. kimberleyensis* is 0.901. As with the previous difference it is not likely that this is an ontogenetic feature. Juvenile skulls of other labyrithodonts are always shorter and broader than the larger skulls.

The posterior border of the external naris is angular in *D. pustulatus.* It is straight across in *D. kimberleyensis.*

The bones of the skull roofs show minor differences which in themselves would not justify the erection of a new species. However, they tend to support the separation based on the above characters. The supratemporal of *D. pustulatus* is narrower and has a less extensive suture with the postparietal. The anterolateral corner of the parietal does not project forward between the frontal and postfrontal as is the case in *D. kimberleyensis.* The posterior border of the postorbital is straight in *D. pustulatus* and sigmoid on *D. kimberleyensis.* In *D. kim-*

berleyensis the nasal-frontal suture is roughly perpendicular to the median suture; in *D. pustulatus* it is oblique.

Comparison of Deltasaurus with related genera

The holotype and only material of *Rhytidosteus capensis* Owen includes three portions of the skull, several parts of the lower jaw rami and a clavicular fragment. The largest skull portion consists of the dorsal and palatal surfaces of the entire antorbital region. The second portion is the interotic part of the skull roof which includes most of the tabular horns. The third portion is a piece of the right exoccipital which includes the condyle.
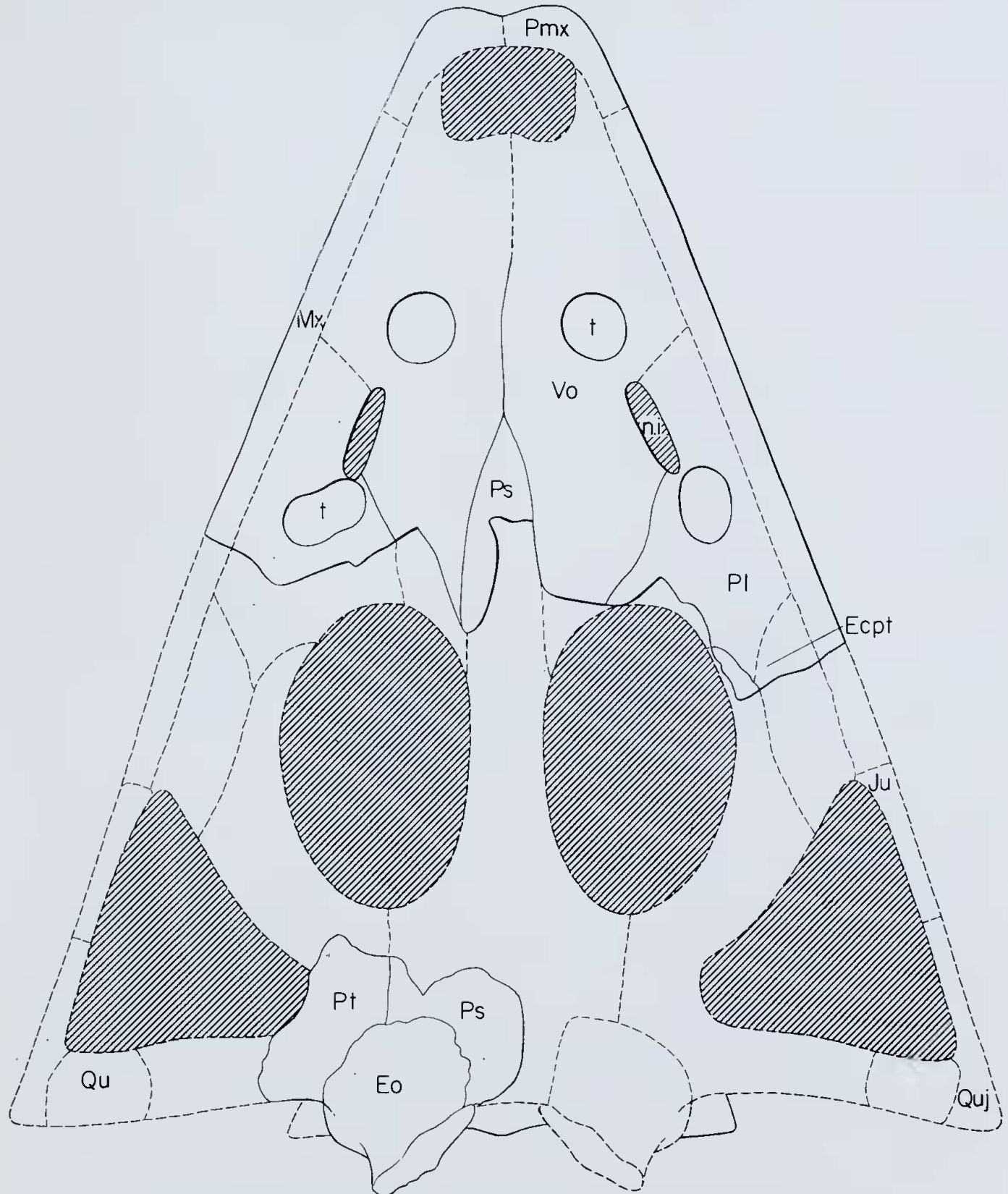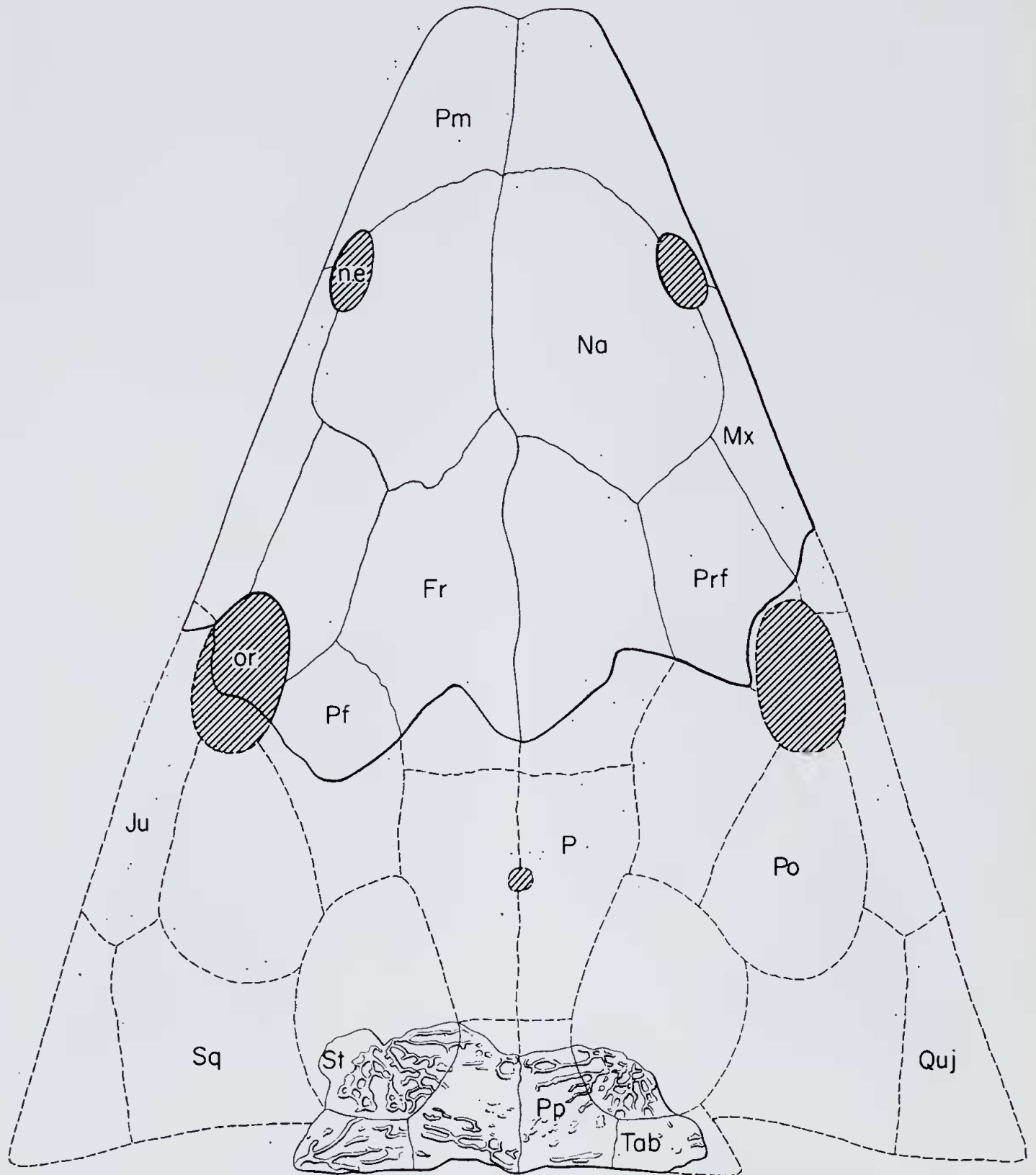

Fig. 12.—*Rhytidosteus capensis* Owen, reconstruction of the dorsal surface of type specimen; antorbital fragment from Owen (1884, pl. XVI); interotic fragment from a plaster replica in U.C.M.P. collection of Brit. Mus. (Nat. Hist.) no. R 503. x 0.58.

R. capensis was collected nearly a century ago near Beersheba, Orange Free State. Owen (1884, pp. 333-338, pls. XVI and XVII) described and figured the antorbital portion and the lower jaws. A central piece of the left lower jaw is missing and the contact shown by Owen (pl. XVII) is obviously not the natural one. As Romer (1947, p. 190) has pointed out, the distance from the glenoid fossa to the symyhysis in Owen's reconstruction is far too short for the length of the antorbital region of the skull. Owen neglected the interotic and exoccipital portions. The exoccipital was described and figured by Watson (1919, pp. 35-36, fig. 21).

Fig. 13.—*Rhytidosteus capensis* Owen, reconstruction of the palatal surface of the type specimen; antorbital fragment from Owen (1884, pl. XVII); basicranial fragment from a plaster replica in the U.C.M.P. collection of Brit. Mus. (Nat. Hist.) no. R 503. x 0.58.

The British Museum responded generously to a request for further information and loaned plaster replicas of the exoccipital and unillustrated fragments to the University of California Museum of Paleontology.

Comparisons with *D. kimberleyensis* show that the interotic and exoccipital fragments are comparable in size with the antorbital portion of the skull. They were undoubtedly derived from the same individual. New restorations of the dorsal and palatal surfaces are attempted (figs. 12 and 13). The interotic portion has most of the postparietals and tabulars and the posterior edges of the supratemporals. The position of this fragment in the restoration was determined by roughly estimating the size of the missing parietal bones and the distance of the tabular horn from the missing posterolateral skull corner. Owen's plate XVI shows that the left half of the antorbital portion is crushed; it has been restored to correspond in shape with the right side.

Many details of the *R. capensis* fragments relate this form to *D. kimberleyensis*. The orbit and naris lie close to the lateral edge of the skull. The orbit faces outward as well as upward. There is no lacrimal bone. The supraorbital groove has a similar course in the antorbital region. The skull table is nearly flat between the tabular horns and the cheek probably descended steeply to the quadrate region. The tabular horn is small and sharply angular. The surface ornament of *R. capensis*, although coarser in texture, has the fundamental structure of *D. kimberleyensis*: the bifurcating radial ridges have a higher relief than the concentric ridges; nodes along each radial ridge mark conjunctions with the concentric ridges; pitted and grooved areas are irregularly arranged on each bone.

The palate surface is completely covered with a dense shagreen of tiny denticles. The cultriform process is broad and has a conical termination between the vomers. The choana, although more regularly oval than that of *D. kimberleyensis*, is also set well in from the lateral margin of the skull. The fossae for the vomerine and palatine tusks are similarly placed relative to the choana.

The conjoined lower jaw rami form a bulbous symphysial shelf which fits within the margins of the upper jaw. The ventral borders of the rami are sharply keeled posteriorly. The retroarticular processes are similar in relative size to those of *D. kimberleyensis* and the outlines of the glenoid facet and the adductor fossa correspond closely. These characters of the lower jaws also indicate a close relationship of the African and Australian genera.

A number of characters of the skull and lower jaw distinguish *R. capensis* from *D. kimberleyensis*. *R. capensis* has a longer and narrower antorbital region of the skull. The external naris is set further back from the snout tip. The anterior part of the postparietal is indented by the posterior margin of the supratemporal. The supraorbital groove is less well defined.

The left side of the antorbital fragment of *R. capensis* appears to be broken off just anterior to the forward edge of the interpterygoid vacuity.

The portion of the palate anterior to the vacuity is relatively much longer than it is in *D. kimberleyensis*. As restored, the interpterygoid vacuities of *R. capensis* are proportionately much smaller than those of *D. kimberleyensis*. In *R. capensis* the orbit lies above and lateral to the anterior part of the interpterygoid vacuity; in *D. kimberleyensis* the orbit is above and lateral to the center of the vacuity.

The lower jaw of *R. capensis* is deeper and more massive than that of *D. kimberleyensis*. The posterior edge of the retroarticular process is notched whereas it is pointed in *D. kimberleyensis*.

Romer (1947, p. 190, fig. 34) referred *Microposaurus casei* (Haughton, 1925, pp. 253-256, figs. 17-18) to *R. capensis* and made a composite restoration of the two skulls. He considered the common horizon and the similarity of the skull shape and size to be indicative of identity and the lateral orbit and naris of *R. capensis* and the posteriorly placed quadrates of *M. casei* to be the results of differential distortion.

By including the interotic fragment of *R. capensis*, a restoration of the dorsal surface which differs materially from Romer's composite has been produced. The broad cultriform process and the extensive exoccipital-pterygoid suture suggest that *R. capensis*, unlike *Microposaurus casei*, is unrelated to the trematosaurs.

M. casei displays such typical trematosaur characters as a greatly extended postorbital region, a very long parasphenoid-pterygoid suture, a narrow cultriform process and a double anterior palatal vacuity. The parasphenoid probably extensively underplates the exoccipitals as in other trematosaurs.

"Trematosaurus" kannemeyeri (Broom, 1909, pp. 270-271) has tentatively been referred to *R. capensis* by Kitching (1957, p. 81). Broom did not illustrate the specimen but von Huene (1920, fig. 8) contributed an interpretation restored from the measurements cited by Broom. The skull is very narrow in the orbital region. This fact alone suggests that *"T." kannemeyeri* should be retained in the Trematosauridae. The generic designation, however, is probably not correct.

Plaster and rubber replicas of the holotype skulls of *P. erici* and *P. wimani,* generously donated by the Paleontological Institute, University of Uppsala, have augmented the excellent review of the genus by Nilsson (1946) and have made direct comparisons with the Australian genus possible. Nilsson's careful reconstructions have been of great value in this work.

Peltostega has long been a problematic genus. It has been variously classified in the Trematosauridae, the Metoposauridae, the Sclerocephalidae and in its own family, Peltostegidae. Wiman (1916, pp. 210-216, text figs. 1-3, pl. XV, figs. 1-3, pl. XVI, fig. 1) first described the type and only specimen of *P. erici*. It was recovered from the Triassic Posidonomya beds of Mt. Anderson, Spitzbergen with *Aphaneramma rostratum* and *Lyrocephalus euri* by the third Swedish Spitzbergen expedition in 1915.

The specimen is the posterior half of a large skull (33-34cm. in median length as restored by

Nilsson, 1946). The postorbital part of the skull roof, the entire occipital surface and part of the palate are preserved. The original restorations of the missing portions of the skull by Wiman are too foreshortened in the antorbital region. The battered condition of the palate (Wiman, pl. XV, fig. 2) led Romer (1947, p. 189) to the conclusion that the structure identified by Wiman as the cultriform process of the parasphenoid was actually the ventral surface of the overlying sphenethmoid. He suggested that the cultriform process had been a narrow structure as in trematosaurids. Nilsson, however, identified the structure as a cultriform process and it is probable that this interpretation is correct.

Nilsson (pp. 4-34) described a second species, *P. wimani*, from the same horizon in Spitzbergen. The holotype, another occipital portion, was found at Mt. Wallenberg. A referred skull roof fragment was found at Mt. Congress. The holotype of *P. wimani* is even larger than that of *P. erici* and differs from it in its comparatively delicate ornament of the dorsal surface, proportionately greater exoccipital condyles and in details of the bones of the skull roof.

Many characters relate *Peltostega* to *Deltasaurus*. Both genera have broad triangular skulls and lateral orbits facing outward as well as upward near the middle of the lateral margins. The parietal foramen of *P. erici* is close behind a line between the posterior borders of the orbits as in *D. pustulatus*. Angular otic notches are present in *D. kimberleyensis* and in both species of *Peltostega*. The frontal bone is excluded from the orbital border in *P. erici* and in both species of *Deltasaurus*.

The dermal sculpture of *Peltostega* corresponds closely to that of *D. kimberleyensis*. The resemblance of sculpture to that of *D. pustulatus* is less obvious, but as noted above, the sculpture of this species is reasonably regarded as a modification of that of *D. kimberleyensis*. The skull roof bones of the *Peltostega* specimens are uniformly pitted over most of their surfaces. These pits are small and equidimensional as in *D. kimberleyensis* but are somewhat more distinct as the concentric ridges of sculpture have a higher relief than in the Australian form. As in *D. kimberleyensis* there is a basic pattern of radiating ridges which carries small rounded nodes at points of bifurcation and at points of junction with the concentric ridges. The peripheries of certain bones of *P. wimani*, notably the anterior edges of the left squamosal and left quadratojugal, have exceptional development of the radiating ridges and the pits are poorly developed or lacking due to imperfect development of the concentric ridges; similar unpitted areas also occur on the type skull of *D. kimberleyensis* as noted in the descriptive section.

Common characters of the posterior part of the palatal surface include broad cultriform processes and broad corpi of the parasphenoid bones and broad posterior margins of the interpterygoid vacuities.

The occipital surfaces of *P. erici* and *D. kimberleyensis* are somewhat similar. The supra-

occipital fenestrae are round and are larger than the foramina magni. The cheeks slope down sharply from the flat skull table. The descending processes of the squamosal are separated from the ascending processes of the pterygoids by long, narrow palatoquadrate fissures.

Peltostega has a longer and narrower antorbital region (as reconstructed by Nilsson), and the posterior margin of the skull table is more strongly excavated. The lateral line system is not as conspicuously developed in *Peltostega;* the supraorbital groove is not continuous medial to the orbit of *P. erici;* and the supratemporal groove of this species is shorter; *P. wimani* seemingly lacks an occipital groove while that of *P. erici* is discontinuous. Both species of *Peltostega* have a posterior bifurcation of the jugal groove not present in *D. kimberleyensis*.

The palatal shagreen of *P. erici* is apparently quite rudimentary although this may be the result of incomplete preservation. The skull has a few small denticles on the pterygoid bone and a row of larger teeth on the posterior part of the left ectopterygoid; these latter are probably also part of the shagreen as they are too irregularly orientated and too medial to be part of a palatal tooth row.

The basicranial regions of *Peltostega erici* and *D. kimberleyensis* show minor differences in construction. The parasphenoid-pterygoid suture is more lateral in *D. kimberleyensis*. The quadrate ramus of the pterygoid is broader and shorter in *P. erici*. The Australian species lacks the large rounded excavation of the posterior margin of the palate between the exoccipital and quadrate condyles. *P. erici* has a small projection of the pterygoid on the posterior margin of the interpterygoid vacuity; this is not present on the outline of the pterygoid which is well-preserved on U.C.M.P. no. 61063.

The only notable difference of the occipital surface is the construction of the subotic process of the exoccipital. This is a broad, flat, obliquely orientated structure in *D. kimberleyensis*. It is a short vertical bar just ventrolateral to the condyle in *P. erici* and *P. wimani*.

The incompleteness of the *Peltostega* and *Rhytidosteus* material has made it impossible to determine if either is more closely related to *Deltasaurus* than the other. *Deltasaurus* and *Rhytidosteus* share a great intensification of the shagreen of the palate, but this may also have been true of *Peltostega*. The dermal sculpture is basically similar in the three genera; that of *Rhytidosteus* is somewhat coarser than that of *Deltasaurus* and that of *Peltostega* is somewhat finer. *Peltostega* is perhaps the most primitive genus in one respect: it lacks a suture between the exoccipital and the pterygoid on the palate. *Deltasaurus* has a short exoccipital-pterygoid suture and *Rhytidosteus* has an extensive one. If the Rhytidosteidae follow the trend found in the Capitosauridae and Brachyopidae described by Watson (1919, 1951, 1956), this sutural contract would be progressively enlarged through evolution.

Comparisons of the Rhytidosteidae with other families

The Rhytidosteidae superficially resemble several genera of the Trematosauridae, particularly *Lyrocephalus,* in the triangular shape of the skull, in the relatively small interpterygoid vacuities and in the positions of the orbits near the levels of the sagittal midpoints. Nilsson (1946) distinguished the Trematosauridae from *Peltostega* by the elongation of the skull between the orbits and the parietal foramen, by the deeper occiput, by the exceedingly high narrow cultriform process and by the great length of the corpus of the parasphenoid, which reaches back to underplate the exoccipital condyles. These characters distinguish the Trematosauridae from the Rhytidosteidae. The double anterior palatal vacuities of trematosaurids is an additional difference.

Nilsson noted the following characters of the Capitosaurids which distinguish this family from *Peltostega:* the otic notch is deeper and narrower; the orbits are placed in the posterior portion of the skull roof; the cultriform process is not wide and it often has a keeled ventral surface; the pteroccipital foramen is not as well defined; and there is a high sharp oblique ridge on the ascending process of the pterygoid (lacking, however, in *Paracyclotosaurus).* These are also valid differences of this family from the Rhytidosteidae.

Capitosaurids and Rhytidosteids share vertical occiputs and differ from the trematosaurids and metoposaurids in this respect. The retroarticular process is similar in shape in the two families. Some of the rhytidosteid genera parrallel characters found in certain capitosaurids. *Deltasaurus* has a single anterior palatal vacuity, similar in shape to that of *Paratosaurus* and *Cyclotosaurus.* There is a palatoquadrate fissure between the squamosal and the pterygoid on the occiputs of *Deltasaurus, Peltostega* and *Parotosaurus. Deltasaurus* and *Rhytidosteus* have an exoccipitalpterygoid suture as do *Cyclotosaurus* and *Paracyclotosaurus.*

Nilsson remarked on the superficial similarities of *Peltostega* and the metoposaurids in the lateral positions of the orbits and the broad cultriform processes. The metoposaurid orbit, however, does not face dorsolaterally as is the case in *Peltostega* and the cultriform process is narrow between the vomers in metoposaurids. The metoposaurid cultriform process passes broadly and evenly into the corpus of the parasphenoid; the corpus expands suddenly in *Peltostega.*

Nilsson distinguished the metoposaurids from *Peltostega* by the anterior positions of the orbits, by the enlarged postorbital regions, by the enlarged paraquadrate foramina and by the reduced posttemporal fossae of this family. These distinctions are also valid for the other rhytidosteid genera.

Additional metoposaurid characters not found in the rhytidosteid genera are occiputs which slope down and back from the skull roof and complex (and poorly understood) relations of the pterygoids and squamosals on the cheek portions of the occiputs.

The Brachyopidae share only general labyrinthodont characters with the Rhytidosteidae.

The Rhytidosteidae are a conservative family and retain many primitive rhinesuchidlydekkerinid conditions. The palatal shagreen, the locations of the orbits near the centre of the skull, the broad cultriform processes, the short parasphenoid-pterygoid sutures and the locations of the parietal foramina close behind the orbits distinguish the Rhytidosteidae from contemporary early Triassic families and also suggest derivation of this family from the Rhinesuchidae, Lydekkerinidae or Uranocentrodontidae. The undivided anterior palatal vacuity of *Deltasaurus kimberleyensis* and the palatoquadrate fissure of both *D. kimberleyensis and Peltostega erici* are probably also conservative features. All late Permian rhinesuchoids in which the snout region is preserved have a single anterior palatal vacuity. *Lydekkerina huxleyi* (Watson, 1919, fig. 4) and *Limnoiketes palundinatans* (Parrington, 1948, fig. 6B), show palatoquadrate fissures.

The specialized characters of the skull readily distinguish the Rhytidosteidae from the Rhinesuchidae and the Lydekkerinidae and necessitate a superfamial separation. The rhytidosteids have narrower snouts and broader occiputs. The orbits lie near the lateral edge of the skull roof. The sculpture pattern is modified. The quadrate condyles have moved forward relative to the exoccipital condyles. *Deltasaurus, Peltostega* and *Rhytidosteus* have smaller and more angular otic notches than those found in members of the late Permian families. The palatal exposures of the cultriform processes of the parasphenoids of rhinesuchids and lydekkerinids terminate in sharp angles between the vomers. In most genera of these families this termination lies behind the level of the anterior borders of the interpterygoid vacuities. The rhytidosteid cultriform processes reach far forward between the vomers and have broad conical terminations.

Comparison of the Rhytidosteidae with problematic Triassic genera
Laidleria

Laidleria gracilis, recently described by Kitching (1957, pp. 67-82, figs. 16-19), consists of the palatal surface of the skull, the lower jaws and the articulated partial skeleton, and is preserved on a sandstone slab in the Albany Museum, Grahamstown, South Africa. It was found in the Karroo of the eastern Cape Province. The exact stratigraphic provenance is uncertain but it is probably from the Cynognathus zone as it was found just below the Stormberg rocks and as the matrix resembles Cynognathus zone matrix of other localities.

Certain features of the skull and lower jaw are suggestive of the Rhytidosteidae: the skull is triangular and the occiput is very broad; the orbit lies near the lateral border of the skull; the postorbital region is short; the cultriform process is broad; and the symphysis is expanded into a broad plate.

Many details of skull construction prevent an inclusion of *Laidleria* in the Rhytidosteidae.

The cultriform process of the parasphenoid, although broad, tapers to a sharp point anteriorly in contrast to the broad and conical terminations found in *Deltasaurus* and *Rhytidosteus*. The snout is slender and pointed. In Kitching's interpretation, an otic foramen replaces the otic notch (a condition paralleled by *Tertrema* of the Trematosauridae and by *Cyclotosaurus* and *Paracyclotosaurus* of the Capitosauridae). The frontal forms part of the orbital border; palatal shagreen is either absent or is greatly reduced (a small pitted area on each pterygoid may represent shagreen); there is a palatal tooth row (definitely absent in *Deltasaurus*); and the choana lies close to the lateral edge of the skull.

The most profound differences of *Laidleria* from the Rhytidosteidae occur on the occipital surface. The *Laidleria* occiput is very low and is of uniform height from corner to corner. The descending process of the squamosal has sutural contact with the ascending process of the pterygoid. The exoccipital apparently lacks the processes lamellosus and basalis (a condition also found in *Indobrachyops panchetensis* (von Huene and Sahni, 1958) and the foramen magnum cannot be distinguished from the supraoccipital and basioccipital foramina.

Three characters of *Laidleria* are unique among the Labyrinthodontia: the dentary teeth are very large, few in number and widely spaced; the contact of the pterygoid and ectopterygoid in the palate is peculiar—a rounded posterior lapet of the ectopterygoid underlies the anterior extent of the palatal ramus of the pterygoid; the tabular has two sutures with the exoccipital—the usual suture on the paraoccipital bar and an additional suture medial to the posttemporal fossa.

Useful characters for systematic purposes are perhaps present on the skull roof of *Laidleria gracilis* which is still embedded in matrix. The nature of the lateral line system, the position of the parietal foramen and most of the sutural relations of this surface are unknown.

Kitching (fig. 19B) shows sculpture on the skull peripheries and on the labial surfaces of the lower jaws. The illustration does not depict this sculpture clearly, and comparisons with the sculpture of the rhytidosteid genera cannot be made.

The lower jaw symphysis covers the region of the anterior palatal vacuity and the shape of this structure is not known.

Laidleria superficially resembles *Lyrocephalus* in skull shape but the cultriform process of the parasphenoid is too broad for a trematosaur and the parasphenoid lacks the posterior extension which is characteristic of the Trematosauridae. The numerous peculiarities of skull construction exclude this African genus from the other Permian and Triassic families. Laidleria is best placed in its own family, Laidleriidae as Kitching has suggested. However, there is greater resemblance to the Rhytidosteidae than to other families and it may be provisionally included in the Rhytidosteoidea.

Lastiscopus

Wilson (1948, pp. 359-361, pl. 59) described the only known specimen of *Lastiscopus disjunctus*, a poorly preserved skull from the late Triassic Dockum Formation of Texas, and provisionally placed it in a new family, Lastiscopidae. Little could be said of its construction. As Wilson noted (p. 360), the high vault of the skull and the large interpterygoid vacuity suggest the Trematosauridae. He also stated: "The extreme posterior edge of the parasphenoid is missing but there is good evidence in the broken edges of the bone that it at one time covered the ventral surface of the exoccipitals." This condition would also tend to relate *Lastiscopus* to the *Trematosauridae*.

Two characters of the skull suggest the Rhytidosteidae rather than the Trematosauridae. These are the extreme lateral position of the orbit and the short distance between the orbits and the parietal foramen.

It is to be hoped that more evidence establishing the systematic position of this animal will be found. It is the only non-metoposaurid labyrinthodont of the North American late Triassic and if it proves to be either a trematosaurid or a rhytidosteid, it will be the latest known occurrence of its family. For the present the family, Lastiscopidae should be placed as *incertae sedis* among the superfamilies of the Triassic Temnospondyli.

Age relationships

The entire collection of fossil vertebrates from the Blina Shale may be considered as a faunal unit through the occurrence of *Deltasaurus kimberleyensis*. Skull and lower jaw fragments of this animal were found at all the Erskine Range localities although these are spaced over two square miles of area and more than 70 vertical feet of section. Four jaws of *D. kimberleyensis* were collected at the B.M.R. Dry Corner locality and one at U.C.M.P. locality V 6044. There is no evidence of evolutionary change or faunal replacement among the collections from the various localities.

The uniform lithology of the Blina Shale exposures in the Erskine Range is consonant with the uniformity of the faunal content. There are no intraformational disconformities within the measured section at V 6040 and there is no other evidence to indicate a major interruption of the depositional cycle. No lateral or vertical changes in the sedimentary facies suggest the presence of more than one depositional environment.

The microfloras from the Blina and Kockatea Shales establish a general time equivalence for these units within the lower part of the Scythian Stage (Balme, 1963). The presence of species of *Deltasaurus* in both formations supports the correlation. Dickins and McTavish (1963) place the portion of Kockatea Shale which contains *Deltasaurus pustulatus* in the Otoceratan zone. Minor differences in bone sculpture and skull proportions are the only features which distinguish *D. kimberleyensis* from the Kockatea species and it is not likely that the stratigraphic position of the Blina fauna is far removed from the Otoceratan zone.

Although detailed considerations of the age relationships of the Blina fauna are deferred to a subsequent paper certain conclusions should be stated here.

The similarity between *Deltasaurus, Rhytidosteus* and *Peltostega* indicates that the Blina Shale, the Cynognathus zone and the Posidonomya beds are close in time to one another. These correlations are supported by the occurrence in the Blina Shale of a brachyopid which is close to *Batrachosuchus* of the Cynognathus zone and of trematosaurids which are perhaps congeneric with *Aphaneramma* and *Tertrema* of the Posidonomya beds. The Cynognathus zone, in turn, may be equated with the Bunter Formation of Germany, and with Zone VI of the Cis-Uralian region of the U.S.S.R. through the occurrence in these three units of *Parotosaurus* and *Trematosaurus*. The Posidonomya beds contain ammonites and other invertebrates as well as fish and amphibians and the ammonites place the level in the upper part of the Scythian Stage (Spath, 1930 and Frebold, 1939). In all probability, therefore, the time range represented by the Posidonomya beds, the Blina Shale, the Cynognathus zone, the Bunter Formation and Zone VI is contained by the Scythian Stage.

Watson (1942 and 1957) and Romer (1947) considered the Lystrosaurus zone to be the earliest Triassic level in the Beaufort Formation of South Africa. The temnospondyls of this zone, however, are rhinesuchoids, a group which probably contains the ancestors of the younger capitosauroids (Watson, 1962) and rhytidosteoids. The cranial structure of the rhinesuchoids is notably more primitive than that found in the younger superfamilies, indicating an appreciable time lapse from the Lystrosaurus zone to the Cynognathus zone and the Blina Shale. The position of the Blina fauna in the lower part of the Scythian stage and of *Deltasaurus pustulatus* in the basal Otoceratan zone suggests that Cynognathus zone is the earliest Triassic level in the Beaufort Formation and that the Lystrosaurus zone is of late Permian age.

Acknowledgments

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